Population Dynamics of the Major North American Needle-Eating Budworms
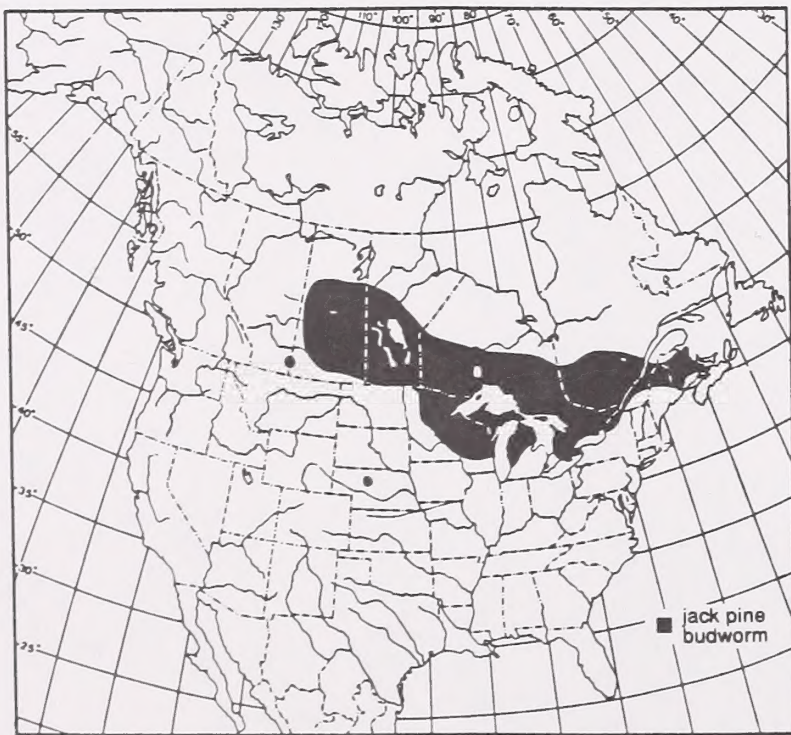
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Distribution of three needle-eating budworms in North America.

Population Dynamics of the Major North American Needle-Eating Budworms

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Abstract

Abstract: Data from six western States provided 1,251 life tables representing western spruce budworm, *Choristoneura occidentalis* Freeman. These data provided projection capabilities for defoliation and successive budworm densities, as well as a basis for comparing survival rates among the three principal North American needle-eating budworms (western and eastern spruce budworms, and the jack pine budworm). Several modifications are suggested in current methods for managing budworm-susceptible forests, and suggestions are provided for further studies on the budworm life systems.

Extended Abstract

The data for this study were collected between 1959 and 1988 from nine projects in six western States (Washington, Oregon, Idaho, Montana, Colorado, and New Mexico). This data base provided both 1,251 life tables and hundreds of additional survival-rate fragments representing populations of the western spruce budworm, *Choristoneura occidentalis* Freeman. These data were analyzed to produce projection capabilities for defoliation and successive budworm densities (eggs, nominal fourth instars, emerging moths, and egg masses) as functions of preceding density, site and stand attributes, interstand influences, systematic year-to-year changes in survival, recent insecticide treatment, and weather.

Some of these results were then used to compare survival rates in western spruce budworm with equivalent rates found in populations of the other principal North American needle-eating budworms—the eastern spruce budworm, *C. fumiferana* (Clem.), and the jack pine budworm, *C. pinus* Freeman.

Across an outbreak, generation survival shows similar declines in the three budworms. For example, in each of the three budworm life systems, predation processes appear to be paramount in maintaining sparse densities. More specifically, in innocuous western spruce budworm populations, the combined effects of predaceous birds and ants provide a low stable equilibrium that can maintain populations at low densities indefinitely, at least in the Pacific Northwest. Apparently, the combined effects of these predators on large larvae and pupae is highest when budworm density reaches about one or two fourth instars per m² of foliage. From this density to about 50 fourth instars per m², average survival from fourth instar to adults increases with increasing density, then declines again (from processes that are not usually related to predation) as density continues to increase. Trends in all three species also are heavily influenced by density-related mass flights by gravid moths.

Other comparisons, however, show that the three life systems differ in some fundamental ways. For example, across a multiyear outbreak, drastic density-dependent reductions occur in the survival rate of small western spruce budworm larvae and also may occur in survival rates of small larvae of the jack pine budworm, but not in the survival rates of the eastern spruce budworm. One consequence is that outbreaks of the western spruce budworm and the jack pine budworm rarely result in significant

overstory mortality, although western spruce budworm outbreaks may destroy a substantial portion of the advance reproduction. Conversely, eastern spruce budworm outbreaks are usually accompanied by extremely heavy overstory mortality of their principal host (balsam fir), but this mortality usually results in the establishment of vigorous new stands. Thus, the principal budworm host would appear to have little evolutionary advantage in the life system of the eastern spruce budworm from investing in chemical defenses. In possible contrast, changes in host foliage seem the most important cause for the systematic reduction in survival across a prolonged western spruce budworm outbreak. More generally, the loss of effective low-density control of the herbivore community by generalist natural enemies in ecosystems in which the dominant vegetation has not evolved effective defenses could lead to both devastation of the host stands and depletion of the foliage-eating guild.

For both the eastern and western spruce budworms, insecticide treatments tend to be more efficacious after outbreaks have persisted for several years. In persistent western spruce budworm outbreaks, for example, both budworm survival and defoliation were lower during posttreatment years in blocks that had been treated with an insecticide. The evidence suggests that the difference in budworm performance between treated and untreated blocks is a function of the difference of host-tree response.

Like those of the needle-eating budworms, the life systems of many other foliage-eating pests include density-related processes that operate through three trophic strata. Because shifts in many such processes are associated with various approximate herbivore density thresholds, density dependence in pestlike life systems might be likened to a density-response stairway with many steps. Clearly, the predator-limitation theory of Hairston and others (1960) is not adequate to explain population limitations in this group of herbivores.

The results of the study provide the basis for several recommendations. First, the site and stand attributes that have predictive value in the life system of the western spruce budworm differ from area to area and commonly are stable only across a limited density range. In light of these results, I suggest several modifications in current models for rating stand hazard and in procedures for appraising defoliation potential and population trend. Second, investigators should carefully examine overall numerical patterns of population change as part of their evaluation of the possible role of any given process in the population dynamics of the species they are studying. Third, planners who deal with budworm-susceptible forests need to develop forest-wide strategies that use a variety of tactical means to cope with the hazards posed by interstand movements of eggs by gravid moths. Fourth, the already high potential value of population-scale historical records would be greatly enhanced by a set of agreed upon sampling protocols. Fifth, comparisons among population trends and age-interval survival rates of three genetically similar needle-eating budworm species suggest many opportunities to optimize the value of individual study results through deliberately comparable studies on all three species. In any case, further studies will be required on each of the separate budworm life systems to fully implement integrated pest management in budworm-susceptible forests.

Contents

List and Definitions of Symbols

The first page where each symbol is mentioned is listed below, together with a definition of the symbol as it is used in this study.

Symbol	Page	Definition
a	26	Intercept in linear regression analysis
AGE	18	Index of stand age (0.75 if < 51 yr; 1.0 if 51-75 yr; 1.25 if 76-150 yr; 1.5 if > 150 yr)
b	26	Slope in regression analysis; in multiple regression, b_1, b_2, and so on
°C	22	Degrees Celsius
cm	3	Centimeter
COLO	7	Colorado Population Study; also used as an index of area (COLO = 1 if a plot is in the Colorado Population Study: else = 0)
DAMAG	8	New Mexico Damage Assessment
DEF	15	Index of defoliation (0.5 + proportion defoliation of current-year foliage)
d.f.	33	Degrees of freedom in variance analysis
DOUG	18	Index of Douglas-fir (0.5 + proportion of the overstory foliage in Douglas-fir)
DST	19	Index of distance to visible defoliation [1.5 - (0.0625 · km to the edge of visible defoliation)]: NOTE: if DST < 0.5, then DST = 0.5
E_{AB}	25	The combined effects of birds and ants on budworm survival across the interval from fourth instar to adults [(N_A on protected trees)/ (N_A on control trees)]
EG	13	Average number of eggs per mass
ELEV	18	Index of elevation [(elevation of the plot)/(elevation of the highest plot in the project)]
EL_i (i=1,5)	18	Index of elevational stratum; if a plot is in stratum i (i = 1,5), then $lnEL_i$ = 1; else $lnEL_i$ = 0 (EL1 represents the plots in the lowest 20 percent of a project's elevational gradient; EL2 represents the next 20 percent; EL3 represents the middle 20 percent; EL4 represents the next 20 percent; and EL5 the highest 20 percent)
exp	21	Base for natural logarithms
°F	22	Degrees Fahrenheit
ft	17	Foot
h	122	Hour
ha	1	Hectare

Symbol	Page	Definition
HI	16	Index of high budworm density (for N_M, HI = 1 if $N_M > 15$; else = 0. For N_E, HI = 1 if $N_E > 500$; else = 0. For N_L, HI = 1 if $N_L > 20$; else = 0. For N_A, HI = 1 if $N_A > 3.5$; else = 0)
HISH	18	Index of shrub density (lnHISH = 1 if shrub density is above average for the area; else = 0)
I	120	Annual trend in egg density ($I = N_{E(n+1)}/N_{E(n)}$)
IDA	9	Idaho Control Project
I_M	141	Annual trend in egg-mass density ($I_M = N_{M(n+1)}/N_{M(n)}$)
in	10	Inch
IPM	158	Integrated pest management
JANT	22	Index of January temperature (lnJANT = 1 if mean January temp < -12.7° C; else = 0)
km	4	Kilometer
ln	18	Natural logarithm
LO	16	Index of low budworm density (for N_M, LO = 1 if $N_M \leq 3.5$; else = 0. For N_E, LO = 1 if $N_E \leq 100$; else = 0. For N_L, LO = 1 if $N_L \leq 4$; else = 0. For N_A, LO = 1 if $N_A \leq 0.7$; else = 0)
m	8	Meter
MART	22	Index of March temperature [mean March temperature (in °F)/29.7]. **NOTE:** average mean March temperature = 1.3 °C
MAYi(i=1,3)	22	Index of May temperature. If temperature is in the indicated range, then lnMAY$_i$ = 1; else = 0. (MAY1 represents mean May temperature below 5.7 °C; MAY2 represents temperatures between 5.7 and 6.8 °C; and MAY3 represents temperatures between 6.8 and 8.8 °C)
MAXR	33	Maximum R^2 Improvement (a technique used in multiple regression)
MED	16	Index of intermediate budworm density (for N_M, MED = 1 if $3.5 < N_M \leq 15$; else = 0. For N_E, MED = 1 if $100 < N_E \leq 500$; else = 0. For N_L, MED = 1 if $4 < N_L \leq 20$; else = 0). For N_A, MED = 1 if $0.7 < N_A \leq 3.5$; else = 0)
mi	17	Mile
min	122	Minute
MONT	9	Montana B.t. Project
n	22	nth generation of the budworm
n-1	22	Budworm generation immediately preceding generation n

Symbol	Page	Definition
N	40	Number of observations
N_A	15	Number of emerging moths per m² of foliage
N_E	16	Number of eggs per m² of foliage
N_L	7	Number of larvae per m² of foliage when most of the insects have molted three times
N_M	7	Number of egg masses per m² of foliage
NMEX	7	New Mexico Suppression Project
N_P	13	Number of living pupae, pupal exuviae, and pupal remains per m² of foliage when adult emergence is about 60-95 percent complete
$N_{(t-1)}$	26	A preceding budworm density
OREG	9	Oregon Population Study
PCP1	22	Index of May rainfall intensity [(observed mean cm of precipitation/ rainy day in May)/0.89]. **NOTE:** (1) a rainy day is defined as a day with $\geq$ 0.25 cm of rain; (2) average mean precipitation per rainy day in May = 0.89 cm in the area of the relevant project
PCP2	22	Index of May and June precipitation (lnPCP2 = 1 if total precipitation for May and June < 8.4 cm; else = 0)
PCP3	23	Index of May, June, and July precipitation (lnPCP3 = 1 if total precipitation for May, June, and July is between 10.5 and 14 cm; else = 0)
PNW	9	PNW Population Study; also used as an index of area (PNW = 1 if a plot is in the PNW Population Study; else = 0)
PROD	18	Index of inherent site productivity (lnPROD = 1 if productivity is rated below average for the area; else = 0)
R	33	Correlation coefficient in multiple regression analysis; R^2 (the coefficient of determination) is the fraction of the variation in the dependent variable that is accounted for by regression
RTMSE	42	Square root of the mean square error, in natural logarithmic form
s	122	Second
S_A	25	Number of egg masses deposited per emerging moth (N_M/N_A). **NOTE:** this rate represents the net influence of both on-site mortality-causing processes and interstand dispersal
SAMP	10	Oregon Sampling Test; also used as an index of area (SAMP = 1 if a plot is in the Oregon Sampling Test; else = 0)
SASP	18	Index of south aspect (lnSASP = 1 if site faces south to southwest; else = 0)

Symbol	Page	Definition
S_G	95	Survival rate from eggs to emerging moths (N_A/N_E)
SIZ	19	Index of outbreak size (0.5 + proportion of a 20 000-ha area around the plot that is visibly defoliated)
SLOPE	18	Index of slope (0.75 if slope is $\leq$ 10 percent; 1.0 if 10 percent < slope $\leq$ 25 percent; 1.25 if < slope $\leq$ 40 percent; 1.5 if slope > 40 percent
S_L	25	Survival rate from nominal fourth instar to emerging moths (N_A/N_L)
SPR	18	Index of spruce (0.5 + proportion of the overstory foliage in spruce)
S_s	25	Survival rate from eggs to nominal fourth instar (N_L/N_E). **NOTE:** this rate represents the net influence of both on-site mortality-causing processes and interstand dispersal
STK	18	Index of stocking (lnSTK = 1 if stocking is average to overstocked for the area; else = 0)
SUMT	22	Index of temperature change from May to June (lnSUMT = 1 if mean June temperature was within 0.8 °C of mean May temperature; else = 0)
TRT	23	Index of insecticide treatment (lnTRT = 1 if the plot is in a treated block; else = 0)
TRUE	18	Index of true fir (0.5 + proportion of the overstory foliage in true fir)
VCD	18	Index of variation in crown depth (0.75 if almost none; 1.0 if below average; 1.25 if about average; 1.5 if above average to extremely variable compared with the other plots in the same study)
WASP	18	Index of west aspect (lnWASP = 1 if site faces west to north; else = 0)
WET	18	Index of site wetness (lnWET = 1 if site wetness is above average for the area; else = 0)
WXBASE	7	Montana Baseline Project
X_i	26	Some attribute or index (i) of the budworm life system
Y_i	26	Some dependent variable (i)
yr	18	Year
YRi(i = 1,n)	23	Index of year (lnYR = 1 if year = year (i); else = 0)
YRIDX	23	Index of year used with the OREG data (1981-88). (If year $\leq$ 1985 then YRIDX = 1; else = 0)

1

Introduction

But the land, and the creatures that go with it, are what is left that is good, and they are the authors of the book that I find worth reading; and anyway, a man has to live according to his lights even if his lights are the red coals in the base of a firepot.

—From "One Man's Meat" by E.B. White (1983)

Notorious among animals are some of our foliage-eating forest insects. Through their sometimes spectacular outbreaks, a few of these pests (for example, gypsy moths, spruce budworms, tent caterpillars) are probably as well-known to the general public as spiders, pigs, and rats. Here, I attempt to use what we have learned about the population dynamics of some of these species to further our own species' age-old struggle to understand and use the natural processes that control animal numbers.

Throughout this paper, the western spruce budworm, *Choristoneura occidentalis* Freeman, called hereafter "western budworm," will be the key foliage-eating insect species to which all others are referenced. Here is a brief résumé of what we know about this pest.

1.1 The Western Budworm

Throughout their range in the interior forests of the Western United States, western budworm populations have for millenia undergone periodic outbreaks, leaving their mark in even the oldest growth rings of sampled trees (Anderson and others 1987, Swetnam and Lynch 1989). During the first half of this century, outbreaks of this pest were small, widely scattered, subsided quickly, and resulted in little or no damage. For the past 40 years, however, outbreaks have been occurring annually on an average of about 2 million ha, which represents about 3 or 4 percent of the approximately 60 million ha of the western forest that is considered susceptible (Stipe 1987). Presumably, suboutbreak populations are present in virtually all of the remaining forest, usually at densities where they are barely discernible by standard sampling techniques. Currently, this pest is the most destructive forest defoliator in western North America (Furniss and Carolin 1977).

In recent years, interest in managing the western budworm has shifted from controlling outbreaks to preventing future ones through judicious forest management (Carlson and others 1985c, Carlson and Wulf 1989). For this reason, a central purpose of this paper is to examine relations between budworm numbers and environmental attributes, including both on-site conditions and indices of interstand influences.

1.2 Seasonal Development

On emergence, adult western budworm females can lay several egg masses. Eggs are laid on host foliage, and Carolin (1987) reported that the moths deposit their first and largest egg masses where they emerge. Similarly, Greenbank and others (1980) reported that females of the spruce budworm, *C. fumiferana* (Clem.), hereafter called eastern budworm, typically lay about half of their eggs at the site where they emerge. Western budworm adults are strong fliers, and I have proposed (Campbell 1987) that redistribution of the population by adult females is a major factor in western budworm population dynamics.

Budworm eggs hatch in about 10 days. In the Pacific Northwest, hatch is usually completed by late August. The first of two major larval dispersals occurs at hatch, as the larvae migrate to hibernation sites—often under bark scales and lichens—and spin hibernaculae.

The second major larval dispersal occurs the following spring. The larvae must move from hibernation sites to foliage, where they tunnel into needles and buds. Subsequently, third instars leave the mined foliage and begin feeding on newly opened vegetative shoots. In Northwest forests, the population passes through fourth instar from about mid-June to early July, depending largely on latitude, longitude, elevation, slope, and aspect.

By fourth instar, the larvae have spun silken feeding tubes in the current-year foliage. Many insects pupate in these tubes; others move toward the bole and pupate on older foliage. The mature larva always spins a network of threads, which surround and cradle the pupa. The pupal interval lasts about two weeks.

Recent information on all aspects of the natural history of the western budworm is summarized in Brookes and others (1987).

2
Objectives and Approach

You can observe a lot by watching.

—Yogi Berra
[in the New York Times, Kaplan (1991)]

2.1 Objectives

The objectives of the study were (1) to describe relations between environmental conditions and subsequent patterns of numerical behavior among populations of the western budworm; (2) to compare survival rates representing outbreaks of the western budworm with those derived during outbreaks of two other budworm species—the eastern budworm in New Brunswick, and the jack pine budworm, *C. pinus* Freeman, in Michigan; (3) to contribute to current understanding of both long-term budworm-forest relations and the processes that determine numbers of foliage-eating insects; (4) to improve current methods for rating stand hazard to the western budworm, appraising defoliation potential, and managing budworm-susceptible forests; and (5) to evaluate the potential utility of historical budworm-related records for researchers, planners, and managers.

2.2 Approach

At a symposium held to consider what to do about the spruce budworm, Knight (1976) suggested that data already recorded should be retrieved and analyzed. My largely retrospective study described in this paper began in 1982, when we realized that western budworm larvae, pupae, emerging moths, and egg masses all exhibit distinct and rather precise intratree patterns of occurrence (Campbell and others 1984a). For population research, the significance of these findings was in the implication that estimates of density drawn from a single stratum (for example, 45-cm tips from midcrown branches) could be used to estimate density on the whole tree.

Because these findings focused my interest on data containing estimates of budworm density, I began a search for data sets that included annual estimates of density at the start of at least two budworm life stages, together with an estimate of defoliation. To be most useful, data representing any given plot had to span at least two years. Fortunately, several projects with just such counts were reaching completion in the early 1980s, and several data sets were also acquired that had been accumulated during earlier years. Altogether, the data base that was assembled includes nine projects and studies, and observations drawn from Washington, Oregon, Idaho, Montana, Colorado, and New Mexico, spanning the 29 years from 1959 to 1988.

To organize the data, each potential predictor was placed in one of the following categories:

Attributes of sites and stands—During the conceptual phase of this study, many investigators were intensely interested in relations among forest attributes and the numerical behavior of the budworm. Unfortunately, empirically based descriptions of such relations were few and fragmented. Thus, no one could specify the attributes that would prove to be related to changes in budworm numbers.

Fortunately, in 1983, an early draft of a generalized indexing model (Wulf and Carlson 1985) provided both a testable first-approximation basis for classifying sites and stands with respect to the budworm, and a reasonable basis for developing a scheme to accumulate information on such attributes. Although Wulf and Carlson's model does not include elevation, reports by two other recent groups of investigators (Heller and Kessler 1985, Stoszek and Mika 1985) confirm earlier findings that correlate elevation with defoliation. These reports stimulated me to incorporate indices of elevation into several of the data sets.

Collectively, the variables in this category include indices of elevation, slope, aspect, wetness, inherent site productivity, overstory composition (Douglas-fir, true fir, and Engelmann spruce), stand age, variation in crown depth, stocking, and shrub density.

Density dependence—Density dependence includes both intraspecific numerical responses by the budworm to the density of its own population, and responses by host trees and natural enemies to factors associated with budworm abundance. The category includes both a sequence of budworm densities (egg masses, fourth instars, residual pupae, and emerging moths) and indices of these densities (low, medium, and high).

Interstand influences—Two indices were developed to test ideas about the influence of outbreak size and proximity on the numerical behavior of budworm cohorts on individual plots. The first index is based on the distance (to a maximum of 16 km) from a plot to the edge of visible defoliation. The other index is based on the visibly defoliated portion of a 20 000-ha area around the plot.

Weather—Several investigators have correlated weather patterns with the area subsequently visibly defoliated by the budworm. Hard and others (1980) found that defoliation in northwestern Montana and northern Idaho varied with weather during May, June, and July of the previous year. Defoliation varied directly with mean maximum temperature and inversely with the frequency of days with measurable precipitation. Twardus (1980) found that warm, dry periods often preceded outbreaks in north-central Washington. Kemp and others (1985) found an inverse relation between mean January temperature and outbreak frequency; they suggested that budworm trends might be influenced by both mean temperatures and highly variable temperatures during the entire winter and spring.

Finding this research suggestive, I used monthly weather summaries (U.S. Department of Commerce 1959-69) to assemble meteorological data to accompany the plot data representing one of the data bases (the Montana Baseline Data [section 3.1.1]). Weather variables examined include temperature data for each month from December through July, and precipitation data for May, June, and July.

Systematic year-to-year differences—Several data sets include a sequence of annual estimates of densities and defoliation on the same plots. By incorporating year indices into these data, I was able to explore them for systematic year-to-year changes.

Influence of insecticide treatment—Three data sets (sections 3.1.3, 3.1.5, and 3.1.7) include observations drawn from both untreated blocks and those that had been treated with an insecticide. By incorporating a treatment index in each of these sets, I was able to test for possible systematic differences in the numerical behavior of the budworm on treated and untreated blocks during several posttreatment years.

With these data in hand, I approached my objectives through an analytical sequence that was designed to produce (within the limits of the data base) a projection capability for each of the following variables: eggs per mass, fourth instars, emerging moths, egg masses, and defoliation.

Literature describing relations between site and stand attributes and the western budworm is summarized and interpreted by Wulf and Cates (1987). They derive 26 indices of susceptibility and vulnerability from "...documented relations between budworm and characteristics of sites and stands." Unfortunately, as these authors note, many site and

stand variables (and, consequently, many of these indices) are correlated. After reviewing this document and related material, I concluded that every attribute of a site or stand that is known to be related to budworm density or defoliation might reflect the net influence of several different underlying processes, and that each of these attributes might also reflect a process (or processes) acting during more than one budworm life stage. From these conclusions, the data base assembled here (section 3.2) clearly does not provide an adequate basis for developing an explicit model of the processes that are important in budworm population dynamics. Rather, the strength of these data lies primarily in two areas: the unusually broad basis they provide to evaluate existing population-related hypotheses, and the clues they provide about important population-related processes.

Relations between the western budworm and forest attributes that are specified in the results are summarized in Chapter 4. To minimize repetition, environmental influences that may be responsible for some of these relations also are noted in this same chapter. In Chapter 5, I discuss long-term budworm-forest relations (section 5.1), the roles and population-scale implications of major processes and environmental modifiers in budworm population dynamics (section 5.2), management considerations (section 5.3), the usefulness of historical records (section 5.4), and study limitations (section 5.5). Chapter 6 describes recommendations for further work, and Chapter 7 provides a summary of the project.

3

Methods and Procedures

We have to face the fact that while ecological work is fascinating to do, it is unbearably dull to read about....

—From "Animal Ecology"
by Charles Elton (1927)

3.1 Study Areas

One data set was gathered primarily by personnel of the Idaho Department of Lands and Forests. Eight other sets were gathered by personnel of the USDA Forest Service, five of which were gathered under the auspices of Forest Pest Management, usually to evaluate the efficacy of an insecticide. The remaining three sets were collected as part of population studies. The location of each project is shown in figure 1.

3.1.1 Montana Baseline Project, 1959-69 (WXBASE)

The Montana Baseline Project was begun by the Intermountain Forest and Range Experiment Station and later became a project of Forest Pest Management in the Northern Region. The objective of the project, directed by T.T. Terrell, was to "...determine the association between budworm populations of the year and defoliation ... the subsequent year" (Terrell 1961).

The project was conducted on 25 single-tree plots, which were widely scattered across southwestern Montana from Ovando on the north (about 47° N. latitude) to Yellowstone National Park on the south (about 44.5° N. latitude), and from Livingston on the east (about 110° W. longitude) to Darby on the west (about 114° W. longitude). According to estimates furnished by S. Tunnock (1983), overstory composition at these plots was dominated by 84 percent Douglas-fir, *Pseudotsuga menziesii* var. *glauca* (Mirb.) Franco, with only about 1 percent true fir, *Abies* spp., and 2 percent Engelmann spruce, *Picea engelmannii* Parry ex Engelm.

Egg-mass density per square meter of foliage (N_M) among the 250 WXBASE plot-years used in this study ranged from zero to 82.4, with a mean of 9.6 ± 13.2 (standard deviation). Average percentage of defoliation of current-year foliage was 28.0 ± 27.0.

3.1.2 Colorado Population Study, 1964-66 (COLO)

The Colorado Population Study, a project of the Rocky Mountain Forest and Range Experiment Station, was directed by M.E. McKnight. The objective was to "...achieve a better understanding of regulators of budworm populations" (McKnight 1971).

The project was conducted on plots in three stands on the San Isabel National Forest, Colorado. In 1983, average overstory composition of these plots included about 65 percent Douglas-fir; 21 percent white fir, *A. concolor* (Gord. and Glend.) Lindl. ex Hildebr.; and 5 percent Engelmann spruce.

Among the 11 COLO plot-years used here, densities of nominal fourth instars per square meter (N_L) ranged from 33.9 to 84.4 with a mean of 55.7 ± 16.5.

3.1.3 New Mexico Suppression Project 1977-83 (NMEX)

The New Mexico Suppression Project of USDA Forest Service, Forest Pest Management, Southwestern Region, was directed by D.L. Parker. Its objectives were to "...suppress the budworm population to as low a level as possible" (by treatment with carbaryl) and to "evaluate prolonged effectiveness of suppressing the...population...by [acquiring] follow-up information...." (Parker and others 1978).

The project was conducted on 12 blocks (6 treated blocks and 6 checks), which totaled 29 939 ha in the Santa Fe National Forest and the Jemez Pueblo Indian Reservation in northern New Mexico.

Figure 1—Project locations: A = WXBASE; B = COLO; C = NMEX; D = DAMAG; E = IDA; F = PNW; G = MONT; H = SAMP; I = OREG.

Budworm densities and defoliation were derived from 300 three-tree cluster plots, 25 of which were distributed in each of the 12 blocks. Average overstory composition included about 35 percent Douglas-fir, 32 percent white fir, and 2 percent Engelmann spruce. Across the 7-year life of this project, observations were discontinued in many of the three-tree clusters. Data documenting conditions in each of the remaining clusters for 1977-80 are reported in Parker and Ragenovich (1980), Parker and others (1979) and Ragenovich and Parker (1981). Telfer (1984) summarized the entire 7-year project.

Nonzero values of N_L per m² among 625 NMEX plot-years ranged from 0.08 to 81.5, with a mean of 10.1 ± 12.2. Average defoliation recorded during 618 plot-years was 21.9 ± 25.9 percent.

**3.1.4
New Mexico Damage
Assessment, 1978-84
(DAMAG)**

The New Mexico Damage Assessment was conducted by the Southwestern Region of Forest Pest Management; data were gathered under C.R. Stein. The project was conducted to "...assess damage to Douglas-fir, true fir, and spruce caused by the western spruce budworm...." (Stein and McDonnell 1982).

The project was conducted in northern New Mexico on 17 0.4-ha plots in the Taos, Questa, and Tres Piedras Ranger Districts of the Carson National Forest. Average overstory composition on these plots included about 55 percent Douglas-fir, 11 percent white fir, and 9 percent Engelmann spruce.

Values of N_L per m² among 68 plot-years in DAMAG ranged from 0.05 to 46.5, with a

mean of 20.2 ± 12.0. Average defoliation recorded during these same plot-years was 69.9 ± 31.0 percent.

**3.1.5
Idaho Control Project,
1979-82 (IDA)**

The Idaho Control Project, which was under the Idaho Department of Lands, was directed by R.L. Livingston. The project was undertaken after the Idaho Department of Lands and the Boise Cascade Corp. had concluded that their timber stands "...were severely threatened [by the budworm] and needed immediate protection" (Livingston and others 1982).

The project was conducted on six blocks (three treated blocks and three checks), which totaled about 80 000 ha in portions of Valley and Boise counties, in west-central Idaho. Two pesticides, carbaryl and acephate were used in the project.

Data to document the project were gathered from 324 three-tree cluster plots. Average overstory composition among these plots included 22 percent Douglas-fir, 46 percent true fir (mostly grand fir, *A. grandis* [Dougl. ex. D. Don] Lindl., plus some subalpine fir, *A. lasiocarpa* [Hook.] Nutt.], and 6 percent Engelmann spruce). Values of N_L per m^2 among 546 plot-years in IDA ranged from 0.22 to 98.7, with a mean of 18.3 ± 13.5.

**3.1.6
PNW Population Study,
1979-82 (PNW)**

The PNW Population Study, a project of the Pacific Northwest Forest and Range Experiment Station, was directed by R.C. Beckwith in Washington, and by T.R. Torgersen and me in Oregon, Idaho, and Montana. The objective of the project was to further understanding of western budworm population dynamics (Campbell and others 1983a).

The study was conducted on 16 5-ha plots in north-central Washington (Methow River Valley and Okanogan highlands), west-central Idaho (near McCall), northeastern Oregon (Wallowa-Whitman National Forest), and northwest Montana (near Seeley Lake). Average overstory composition among the PNW plots included 55 percent Douglas-fir, 18 percent grand fir, and 1 percent Engelmann spruce.

Among the 29 PNW plot-years used here, N_L ranged from 0.2 to 47.7, with a mean of 19.1 ± 15.1.

**3.1.7
Montana B.t. Project,
1981-83 (MONT)**

The Montana B.t. *(Bacillus thuringiensis)* Project was conducted by the Northern Region, Forest Pest Management, and managed by L.E. Stipe. The principal objective of the project was to "...obtain performance data on two registered formulations of B.t. on western spruce budworm...." (Stipe and others 1983).

The project was conducted on nine blocks (six treatment blocks and three checks), which totaled 10 024 ha on the Beaverhead and Deerlodge National Forests and adjacent lands near Butte, Montana. Data used to document MONT were gathered from 225 three-tree cluster plots, 25 of which were distributed in each block.

The overstories in MONT were almost pure Douglas-fir (average 98 percent); N_L per m^2 among 501 plot-years ranged from 0.34 to 52.4, with a mean of 11.1 ± 10.0. Average defoliation was 51.2 ± 26.7 percent.

**3.1.8
Oregon Population
Study, 1981-88 (OREG)**

The Oregon Population Study, directed by T.R. Torgersen, is another project of the Pacific Northwest Research Station. Like preceding population studies, this one is intended to advance understanding of western budworm population dynamics. The study was conducted on 10 5-ha plots in the Blue Mountains of northeastern Oregon. Since about

1981, the mixed conifers in this area have played host to a major outbreak, and this study documents changes in budworm numbers in 8 of the 10 OREG plots for each year from 1983 to 1988. Observations in the two remaining plots commenced in 1986.

Among 53 OREG plot-years, N_L per m^2 ranged from 0.7 to 102.6, with a mean of 30.3 ± 24.1. Records are not available on overstory composition of the OREG plots.

3.1.9
Oregon Sampling Test, 1982 (SAMP)

The Oregon Sampling Test, a project of the Pacific Northwest Region, Forest Pest Management, was directed by D.B. Twardus. The objective was to evaluate sampling plans proposed for estimating budworm numbers.

The study was conducted in the Malheur National Forest in northeastern Oregon. Average overstory composition among the 19 plots included about 46 percent Douglas-fir and 33 percent grand fir. Among these plots, N_L per m^2 ranged from 29.1 to a rather startling 166.5, with a mean of 73.1 ± 40.3.

3.2
Data Collection and Processing

Most of the data used here are unpublished. Copies of all these data are available from the author.

3.2.1
On-Site Densities and Defoliation

The people who produced the data used here invariably estimated both densities and defoliation from sample branches or branch tips drawn from the crowns of host trees. For each project, the number of trees sampled, number of branches or tips drawn per tree, branch tip length, and bases used to express both density and defoliation are summarized in table 1.

3.2.1.1 Sampling precision—Recently, data from the 5-ha plots in the PNW study were used to develop sequential count plans for nominal fourth instars and egg masses (fig. 2) (Campbell 1988). To develop these plans, I used Iwao and Kuno's (1968) method to estimate the relation between the mean and the variance and Kuno's (1969) formula to calculate sample size. Because these plans were developed from counts on 5-ha plots, they provide a conservative basis for estimating sampling precision (expressed as the ratio of the standard error of the mean to the mean) in the relatively homogeneous three-tree cluster plots used in several projects. In two projects (PNW and OREG), sample size was adjusted by the original investigators to achieve a precision of about 0.1. Two other projects (COLO and DAMAG) provided estimates derived from a relatively large number of samples. In the remaining projects, the number of sample tips drawn per plot, the generally high budworm densities, and the fact that the samples for any given plot were all drawn from a cluster of reasonably homogeneous trees suggest an average sampling precision of about 0.2 to 0.3 for both egg masses and larvae.

The following summary of procedures used in the various projects and studies was compiled primarily from information in Livingston and others (1982), McKnight (1971), Parker and others (1978), Srivastava and others (1984), Stein and McDonnell (1982), Stipe and others (1983), Terrell (1961), and Terrell and Keefe (1964).

3.2.1.2 Egg masses (N_M)—In all projects, the foliage samples were examined for egg masses in field laboratories. At least three projects (NMEX, DAMAG, and MONT) conducted these examinations under ultraviolet light. In all projects, the procedures used appear similar to those described in Buffam and Carolin (1966).

One project (WXBASE) used 0.645 m^2 (1,000 in^2) of foliage as their basis for expressing egg-mass density, and one (COLO) used 0.0645 m^2 (100 in^2). All other projects reported

Table 1—Sampling protocols in each of 9 projects on western budworm; except as noted, samples were drawn from midcrown branches

Variable estimated	Project	Tree height class (m)	Trees sampled per plot	Tips per tree	Number of tips sampled	Tip length	Basis used to express variable
Egg-masses:							
	WXBASE	Average	1	2	2	Whole branch	1000 in² (0.645 m²)
	COLO	Average	10	2	20	24 in	100 in²
	NMEX	9-15	3	2	6	70 cm	m²
	DAMAG	6-12	10	2	20	70 cm	m²
	IDA	10-15	3	2	6	16 in	m²
	PNW[a]	7-14	≥15	2	≥30	45 cm	m²
	MONT	10-18	3	2	6	70 cm	m²
	OREG	7-14	≥25	2	≥50	45 cm	m²
	SAMP	7-14	3	2	6	45 cm	m²
Nominal fourth instar:							
	COLO	Average	10	2	20	24 in	100 in²
	NMEX	9-15	3	2	6	15 in	100 buds
	DAMAG	6-12	10	2	20	15 in	100 buds
	IDA	10-15	3	2	6	16 in	100 buds
	PNW[a]	7-14	≥15	2	≥30	45 cm	m²
	MONT	10-18	3	4	12	45 cm	100 buds
	OREG	7-14	≥20	2	≥40	45 cm	m²
	SAMP	7-14	3	2	6	45 cm	m²
Residual pupae:							
	COLO	Average	10	2	20	24 in	100 in²
	PNW[a]	7-14	≥15	2	≥30	45 cm	m²
	SAMP[b]	7-14	3	4	12	45 cm	m²
Emerging moths:							
	OREG[b]	7-14	≥41	2	≥82	45 cm	m²
Defoliation:							
	WXBASE	Average	1	4	4	Whole branch	Percent
	NMEX	9-15	3	4	12	27.5 in	6-class
	DAMAG	6-12	10	4	40	70 cm	6-class
	IDA	10-15	3	1	3	16 in	4-class
	MONT	10-18	3	4	12	1/2 45 cm; 1/2 70 cm	6-class

[a] Samples were usually drawn from all vertical crown strata (upper, mid, and lower).
[b] These sample tips were drawn from the lower one-third of the crown.

their estimates of N_M per m² of foliage. To make all estimates comparable, values of N_M reported for WXBASE and COLO were multiplied by 1.55 and 15.5, respectively.

Srivastava and others (1984) found that average egg-mass densities per m² on whole trees can be estimated efficiently by multiplying N_M on midcrown sample tips by 0.82. To facilitate subsequent comparisons among a sequence of densities, the estimates of N_M reported by each project were multiplied by this constant.
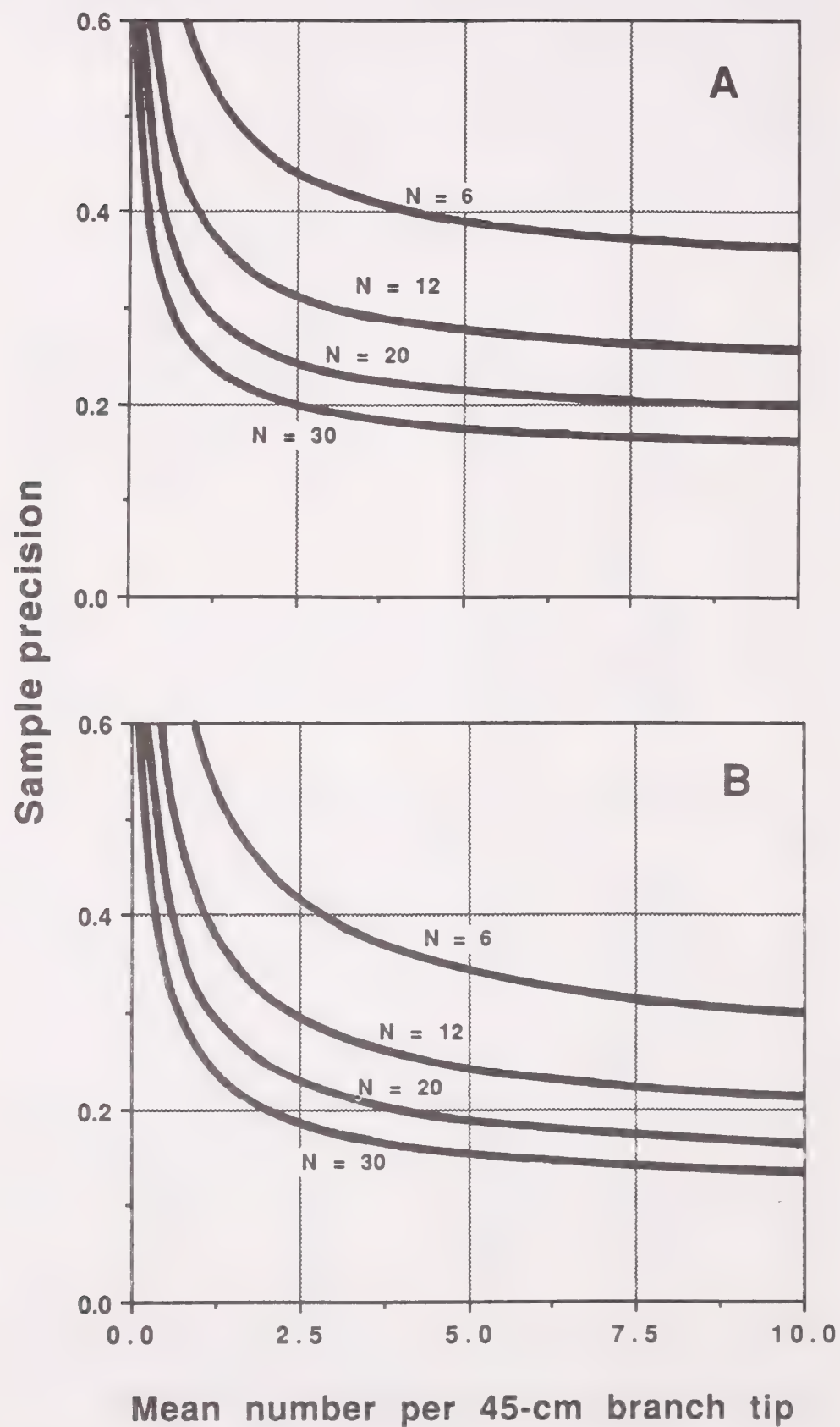
Figure 2—Sampling precision: A, for egg masses; B, for nominal fourth instars. The figure is based on the relation $T_n = (\alpha+1)/[D_o{}^2 - (\beta-1)/n]$ (Kuno 1969). T_n = the cumulative number of egg masses or larvae on the sample foliage; D_o = precision (ratio of standard error of the mean to the mean); n = number of midcrown 45-cm branch tips, α = 0.271 and β = 1.666 (for egg masses); α = 0.688 and β = 1.369 (for larvae).

Mean, minimum, and maximum egg-mass densities found in each project are shown in table 2.

3.2.1.3 Eggs per mass (EG)—In MONT, "...up to two new egg masses per [sample] branch were measured to determine length and the number of rows" (Stipe and others 1983). Subsequently, these measurements were used to estimate the number of eggs per mass (EG) in each plot, by using information in McKnight (1969).

The PNW study also provided direct estimates of EG. These estimates were based on counts of the number of eggs in the egg masses found on sample foliage.

Table 3 shows the mean, minimum, and maximum eggs per mass found in MONT and PNW, as well as observed and calculated means, minimum, and maximum egg densities in each area.

3.2.1.4 Nominal fourth instars (N_L)—All projects examined the foliage samples for larvae in field laboratories. At least four projects (IDA, PNW, MONT, and OREG) facilitated these examinations by using a foliage-beating apparatus similar to that described by Martineau and Benoit (1973).

To make all estimates of N_L comparable, values of N_L per 100 in^2 reported for COLO were multiplied by 15.5. Values of N_L per 100 buds reported for IDA were multiplied by 4.567. (During the Idaho-based portion of the PNW study, we found an average of 456.7 new shoots per m^2 on 45-cm branch tips.) And values of N_L per 100 buds reported for MONT, NMEX, and DAMAG were multiplied by 5.388 because an average of 533.8 new shoots had been found per m^2 during the Montana-based portion of the PNW study.

Srivastava and others (1984) reported that average densities of N_L per m^2 on whole trees can be estimated efficiently by multiplying N_L on midcrown tips by 0.238. Consequently, all estimates of N_L per m^2 on midcrown tips were multiplied by this constant.

Mean, minimum, and maximum nominal fourth instars found in each project are shown in table 4.

3.2.1.5 Residual pupae (N_P)—Residual pupae include all living pupae, pupal exuviae, and pupal remains found on foliage when adult emergence was in progress. In COLO, this sample was drawn when 60 to 80 percent of the moths had emerged. In PNW, OREG, and SAMP, the sample was timed to coincide with about 95-percent adult emergence. To make all estimates comparable, values of N_L per 100 in^2 reported for COLO were multiplied by 15.5.

Srivastava and others (1984) reported that N_P per m^2 on whole trees can be estimated by multiplying N_P on lower crown tips by 0.629. Consequently, estimates of N_P on lower crown tips in SAMP and OREG (the stratum sampled in these studies) were multiplied by this constant.

In COLO, estimates of N_P were based on branch tips drawn from the midcrown. Campbell and others (1984a) reported that pupal densities on midcrown tips could be estimated as 1.781 times the densities on lower crown tips. Consequently, values of N_P on midcrown tips in COLO were multiplied by 0.353 (0.353 ≈ 0.629/1.781), to provide estimates of average N_P per m^2 on whole trees.

Table 2—Budworm egg-mass densities per m² of foliage

Data source	Number of plot-years	Mean value	Standard deviation	Minimum value	Maximum value
Egg-mass density at the start of the budworm generation:					
WXBASE	247	9.63	13.16	0	82.36
NMEX	424	8.92	10.55	0.49	87.49
DAMAG	46	26.41	18.60	0	76.01
IDA	414	3.86	5.68	.08	51.58
PNW	29	4.08	4.15	.28	18.08
MONT	640	22.61	19.48	.80	245.71
OREG	47	8.79	7.25	.49	31.32
Egg-mass density at the end of the budworm generation:					
WXBASE	247	8.85	13.08	0	82.36[b]
COLO[a]	11	10.82	7.13	1.32	26.04
NMEX	394	14.53	19.34	.16	92.91
DAMAG	51	26.47	18.67	0	76.01[b]
IDA	414	4.96	5.82	.08	51.58[b]
PNW	29	5.30	5.73	.12	22.63
MONT	426	35.99	28.16	.83	245.71[b]
OREG	55	7.63	7.18	.08	31.32[b]

[a] To estimate these values, I assumed 40.7 eggs per mass.
[b] Identical starting and ending values indicate projects where the minimum or maximum density was found in a plot at the end of one year and in the same plot at the start of the next.

Table 3—Budworm eggs per mass and egg densities per m² of foliage

Data source	Number of plot-years	Mean value	Standard deviation	Minimum value	Maximum value
Eggs per mass:					
MONT	428	40.7	12.9	6.4	76.2
PNW	29	44.2	9.7	23.0	56.5
Egg density per m² of foliage[a]:					
WXBASE	250	383.8	638.7	0	4,656.3
COLO	11	440.3	290.0	53.8	1,059.8
NMEX	424	330.7	480.3	13.3	5,026.2
DAMAG	46	1,176.1	1,031.8	0	4,200.3
IDA	414	127.8	233.2	2.2	2,514.7
PNW	29	200.7	217.1	9.8	960.2
MONT	428	1,547.5	1,734.5	9.5	12,667.7
OREG	47	303.6	286.2	13.5	1,322.1
SAMP	19	732.4	420.7	252.0	1,554.0

[a] In most locations (WXBASE, NMEX, DAMAG, IDA, and year 3 of MONT), these estimates were based on direct estimates of egg masses, together with estimates of eggs per mass that were derived from an equation.

Table 4—Nominal fourth instars per m² of foliage

Data source	Number of plot-years	Mean value	Standard deviation	Minimum value	Maximum value
COLO	11	55.7	16.5	33.9	84.4
NMEX[a]	324	12.8	12.7	.08	81.5
NMEX[b]	625	10.1	12.2	.08	81.5
DAMAG	51	20.2	2.0	.05	46.5
IDA[a]	414	18.3	14.2	.2	96.45
IDA[b]	546	18.3	13.5	.2	98.7
PNW	29	19.1	15.1	.2	47.7
MONT[a]	428	11.9	10.1	.3	52.4
MONT[b]	501	11.9	10.0	.3	52.4
OREG	53	30.3	24.1	.7	102.6
SAMP	19	73.1	40.3	29.1	166.5

[a] Used in equations as the dependent variable.
[b] Used in equations to project defoliation and residual pupae.

3.2.1.6 Emerging moths (N_A)—The density of emerging moths (N_A) is based on all living pupae and pupal exuviae found on foliage when about 95 percent of the moths have emerged.

Srivastava and others (1984) reported that N_A per m² on whole trees could be estimated by multiplying N_A on lower crown tips by 0.600. Consequently, estimates of N_A on lower crown tips (the basis used in PNW and SAMP) were multiplied by this constant.

Observed or calculated mean, minimum, and maximum densities of emerging moths in each project are shown in table 5.

3.2.1.7 Defoliation (DEF)—Five projects provided estimates of defoliation. In four (WXBASE, NMEX, DAMAG, and MONT), the primary samples were drawn from Douglas-fir. In NMEX, these primary samples were supplemented by samples drawn from white fir in a subset of the plots during the first two years of the project (1977 and 1978). In IDA, about 85 percent of the samples were drawn from grand fir. Three projects (NMEX, DAMAG, and MONT) based their estimates on an indexing scheme by which 25 new shoots on each sample branch were individually examined and assigned one of six defoliation categories. Scatter diagrams (see section 4.4.3.1) show that the IDA defoliation data were categorized by 5-percent increments. Reports for the other project that provided estimates of defoliation (WXBASE) do not describe the method used. For all these projects, I used estimates of percentage of defoliation that had been derived by the original investigators. Mean, minimum, and maximum values of percent defoliation in each project areas are shown in table 6.

Most of the analyses described in Chapter 4 are based on the assumption that linear relations exist between the logarithms of the various variables. To reduce the likelihood that this assumption would not be violated too severely, I used preliminary graphic examinations to search for formulations providing approximately linear relations between lnX and lnY. For variables ranging from zero to 1 (such as proportion of defoliation or proportion of Douglas-fir in the overstory), I found that satisfactory results would be obtained by adding 0.5 to each observation. Consequently, this constant was added to each observation for every such variable. For example, the index of defoliation I use here (DEF) is defined as follows:

DEF = (0.5 + proportion of defoliation of current-year foliage).

Table 5—Observed or calculated emerging moths per m² of foliage[a]

Data source	Number of plot-years	Mean value	Standard deviation	Minimum value	Maximum value
COLO	11	11.5	5.6	4.1	20.7
NMEX	625	2.0	3.2	.002	18.6
DAMAG	51	2.7	2.1	.001	9.8
IDA	546	3.0	3.0	.006	21.0
PNW	29	3.5	3.2	.008	12.5
MONT	501	2.0	2.4	.01	16.0
OREG	49	5.8	5.0	.01	21.7
SAMP	19	7.6	3.3	2.5	13.8

[a] Estimates of the density of emerging moths in IDA, NMEX, MONT, DAMAG, and SAMP are derived from an equation.

Table 6—Percent defoliation of current-year foliage

Data source	Number of plot-years	Mean value	Standard deviation	Minimum value	Maximum value
WXBASE	247	28.0	27.0	0.3	100.0
NMEX	618	21.9	25.9	0	99.2
DAMAG	51	69.9	31.0	1.4	99.9
IDA	315	42.8	29.0	0	95.0
MONT	642	51.2	26.7	4.5	100.0

3.2.1.8 Indices of on-site density—Preliminary examination suggested that numerical relations between the budworm and relevant attributes in its environment might shift significantly across a sufficiently wide range in budworm density. Consequently, to facilitate subsequent examinations of budworm-forest relations in each of the three largest data sets (IDA, MONT, and NMEX), indices of low (LO), intermediate (MED), and high density (HI) were defined as:

- For N_M = number of egg masses per m²:
     LO = 1 if $N_M \leq 3.5$; else = 0
     MED = 1 if $3.5 < N_M \leq 15$; else = 0
     HI = 1 if $15 < N_M$; else = 0.

- For N_E = number of eggs per m²:
     LO = 1 if $N_E \leq 100$; else = 0
     MED = 1 if $100 < N_E \leq 500$; else = 0
     HI = 1 if $500 < N_E$; else = 0.

- For N_L = number of fourth instars per m²:
     LO = 1 if $N_L \leq 4$; else = 0
     MED = 1 if $4 < N_L \leq 20$; else = 0
     HI = 1 if $20 < N_L$; else = 0.

- For N_A = number of emerging moths per m²:
     LO = 1 if $N_A \leq 0.7$; else = 0
     MED = 1 if $0.7 < N_A \leq 3.5$; else = 0
     HI = 1 if $3.5 < N_A$; else = 0.

3.2.2
Site and Stand
Attributes

Working largely from a 1983 draft version of Wulf and Carlson's (1985) generalized indexing model, I sought the following information from every plot in each study area except WXBASE and OREG:

1. Percentage of forest and percentage of host type in an 8-km (5-mi) radius.

2. Physiography (ridge, upper slope, midslope, lower slope, bench or flat, or stream bottom).

3. Slope.

4. Aspect (north-facing, northeast-facing, east-facing, southeast-facing, south-facing, southwest-facing, west-facing, northwest-facing, or no aspect).

5. Temperature characteristics from warmest (1) to coldest (5), compared with the other plots in the same study.

6. Wetness characteristics from driest (1) to wettest (5), compared with the other plots in the same study.

7. Habitat group (cold subalpine fir; cool, moist spruce or subalpine fir; warm, wet grand or white fir; redcedar, western hemlock, or subalpine fir; cold Douglas-fir, grand fir, or white fir; cold, dry spruce or subalpine fir; moist grand fir or white fir; warm, moist spruce or subalpine fir; mesic Douglas-fir; dry grand fir or white fir; warm, mesic spruce; warm, dry subalpine fir; or warm dry Douglas-fir).

8. Percent of the total crown in Douglas-fir, true fir, spruce, larch, and other species.

9. Stand age, years (less than 26; 26-50; 51-75; 76-150, or more than 150).

10. Stand height.

11. Variation in crown depth from almost none (1) to extremely variable (5), compared with the other plots in the same study.

12. Stocking from greatly understocked (1) to overstocked (5), compared with the other plots in the same study.

13. Shrub cover from shrubs virtually absent (1) to extremely high (5), compared with the other plots in the same study.

14. Woody debris from essentially absent (1) to extremely high (5), compared with the other plots in the same study.

15. Inherent site productivity from very poor (1) to excellent (5), compared with the other plots in the same study.

A few plots in NMEX and IDA could not be relocated. Every other plot in each project area (except WXBASE and OREG) was located and classified in 1983, with respect to each of the above site and stand characteristics.

Plot elevations were not estimated in several data sets because of limitations imposed by the small number of plots, their narrow elevational range, or their widely scattered locations. In the remaining data sets, contour maps were used to estimate the elevation of each plot. Ranges in plot elevations within each of these four projects are as follows:

IDA: 1219-2207 m (4000-7240 ft);
MONT: 1725-2164 m (5660-7100 ft);
NMEX: 2377-3018 m (7800-9900 ft); and
DAMAG: 2438-2950 m (8000-9680 ft).

Preliminary analyses revealed that some of the variation in budworm survival rates could be associated with indices of either habitat group or elevation, slope, and aspect, but not with both. Because the two ways of expressing site conditions appear to be redundant, and because the latter indices were most consistently related to survival, indices of habitat group were dropped from further consideration. As the study progressed, a significant correlation was found between each of the following indices and at least one attribute of the budworm population:

ELEV = index of elevation (elevation of the plot)/(elevation of the highest plot in the project).

EL1 = index of the lowest 20 percent of an elevational gradient (lnEL1 = 1 if the plot is in the bottom 20 percent of the gradient; else = 0).

EL2 = index of the next 20 percent of a gradient (lnEL2 = 1 if the plot is in the next 20 percent of the gradient; else = 0).

EL3 = index of the middle 20 percent of a gradient (lnEL3 = 1 if the plot is in the middle 20 percent of the gradient; else = 0).

EL4 = index of the next 20 percent of a gradient (lnEL4 = 1 if the plot is in the next 20 percent of a gradient; else = 0).

EL5 = index of the top 20 percent of a gradient (lnEL5 = 1 if the plot is in the top 20 percent of the gradient; else = 0).

SLOPE = index of slope (0.75 if slope is $\leq$ 10 percent; 1.0 if 10 percent < slope $\leq$ 25 percent; 1.25 if 25 percent < slope $\leq$ 40 percent; 1.50 if slope > 40 percent).

SASP = index of south aspect (lnSASP = 1 if site faces south to southwest; else = 0).

WASP = index of west aspect (lnWASP = 1 if site faces west to north; else = 0).

WET = index of site wetness (lnWET = 1 if site wetness is above average for the area; else = 0).

PROD = index of inherent site productivity (lnPROD = 1 if productivity is rated below average for the area; else = 0).

DOUG = 0.5 + proportion of the overstory foliage in Douglas-fir.

TRUE = 0.5 + proportion of the overstory foliage in true fir.

SPR = 0.5 + proportion of the overstory foliage in Engelmann spruce.

AGE = index of stand age (0.75 if < 51 yr; 1.0 if 51-75 yr; 1.25 if 76-150 yr; 1.50 if > 150 yr).

VCD = index of variation in crown depth (0.75 if almost none; 1.0 if below average; 1.25 if average; 1.50 if above average to extremely variable, compared with the other plots in the same study).

STK = index of stocking (lnSTK = 1 if stocking is average to overstocked for the area; else = 0).

HISH = index of shrub density (lnHISH = 1 if shrub density is above average for the area; else = 0).

Attributes of site and stand indices in each project are summarized in tables 7-10.

Table 7—Attributes of stand indices that have only two possible values (exp and 1)

Index	Data source	Total plot-years	Proportion of total plot-years where index=exp
STK	COLO	11	1.00
	NMEX	992	.49
	DAMAG	51	.50
	IDA	564	.65
	PNW	29	.62
	MONT	642	.43
	SAMP	19	.95
HISH	COLO	11	0
	NMEX	992	.24
	DAMAG	51	.29
	IDA	564	.36
	PNW	29	.34
	MONT	642	.46
	SAMP	19	.16

3.2.3 Indices of Interstand Influences

To develop these indices, I used a series of aerial sketch maps of visible defoliation. Unfortunately, the available maps were sufficient only to provide adequate estimates of the distance to visible defoliation for the IDA plots. Estimates of a second index, one for outbreak size, were derived for all of the plot-years in IDA and most of the plot-years in WXBASE. Each of these indices was significantly correlated with one or more attributes of the budworm population:

DST = index of distance to visible defoliation (1.5 - 0.0625 · km to the edge of visible defoliation). **Note:** If DST < 0.5, then DST = 0.5.

SIZ = index of outbreak size (0.5 + proportion of a 20 000-ha area around the plot that is visibly defoliated).

Attributes of these indices are summarized in table 11.

3.2.4 Meteorological Data

The Montana Baseline Project (WXBASE) includes data collected for 11 successive years from the same 25 widely scattered plots. These data seemed to provide a reasonable basis for developing a first-approximation equation for relating weather to budworm survival. Weather stations used in conjunction with these plots are shown in table 12.

Preliminary analyses suggested that nonlinear relations might be common between budworm density and both mean monthly temperature and monthly precipitation. Consequently, indices were developed that describe monthly temperature and precipitation in relation to both their average values and their extremes. By this process, I was able to test specific conditions for significant associations with changes in budworm numbers.

Each of the following weather indices was significantly correlated with year-to-year changes in egg density in WXBASE:

JANT = index of January temperature (lnJANT = 1 if mean January temperature < -12.7 °C; else = 0).

(text continues on page 22)

Table 8—Attributes of stand indices[a] that have 4 possible values or that can be continuous between zero and 1

Index	Data source	Number of plot-years	Mean	Standard deviation	Minimum value	Maximum value
DOUG	COLO	11	0.65	0.09	0.60	0.80
	NMEX	992	.35	.14	.05	.70
	DAMAG	51	.55	.26	.20	.90
	IDA	564	.22	.13	0	.75
	PNW	29	.55	.23	.20	.90
	MONT	642	.98	.05	.60	1.00
	SAMP	19	.46	.12	.24	.70
TRUE	COLO	11	.21	.08	.10	.30
	NMEX	992	.32	.17	0	.80
	DAMAG	51	.11	.10	0	.30
	IDA	564	.46	.19	0	.90
	PNW	29	.18	.21	0	.55
	MONT	640	0	0	0	0
	SAMP	19	.33	.19	.01	.75
SPR	COLO	11	.05	.04	0	.10
	NMEX	992	.02	.08	0	.60
	DAMAG	5	.09	.16	0	.60
	IDA	564	.06	.08	0	.40
	PNW	29	.01	.01	0	.05
	MONT	642	0	0	0	0
	SAMP	11	0	0	0	0
VCD	COLO	11	.43	.25	.25	.75
	NMEX	992	.51	.21	.25	1.00
	DAMAG	51	.44	.18	.25	.75
	IDA	564	.46	.19	.25	1.00
	PNW	29	.52	.20	.25	1.00
	MONT	642	.55	.16	.25	1.00
	SAMP	19	.53	.16	.25	.75
AGE	COLO	11	.75	0	.75	.75
	NMEX	992	.56	.13	.25	1.00
	DAMAG	51	.68	.17	.50	1.00
	IDA	564	.41	.17	.25	1.00
	PNW	29	.50	.09	.25	.75
	MONT	642	.51	.23	.25	1.00
	SAMP	19	.49	.13	.25	.75

[a] The index equals the value of the attribute plus 0.5.

Table 9—Attributes of stand indices that have only two possible values (exp and 1)

Index	Data source	Total plot-years	Proportion of total plot-years where index=exp
WET	COLO	11	0
	NMEX	992	0.25
	DAMAG	51	.24
	IDA	564	.25
	PNW	29	.28
	MONT	642	.23
	SAMP	19	.53
PROD	COLO	11	.73
	NMEX	992	.22
	DAMAG	51	.14
	IDA	564	.12
	PNW	29	.76
	MONT	642	.57
	SAMP	19	.84
SASP	COLO	11	0
	NMEX	992	.19
	DAMAG	51	0
	IDA	564	.19
	PNW	29	.10
	MONT	642	.23
	SAMP	19	0
WASP	COLO	11	0
	NMEX	992	.15
	DAMAG	51	.24
	IDA	564	.15
	PNW	29	.31
	MONT	642	.03
	SAMP	19	0
EL1	NMEX	896	.16
	DAMAG	51	.06
	IDA	564	.01
	MONT	642	.10
EL2	NMEX	896	.44
	DAMAG	51	.06
	IDA	564	.23
	MONT	642	.31
EL3	NMEX	896	.25
	DAMAG	51	.29
	IDA	564	.53
	MONT	642	.31
EL4	NMEX	896	.13
	DAMAG	51	.41
	IDA	564	.20
	MONT	642	.20
EL5	NMEX	896	.02
	DAMAG	51	.18
	IDA	564	.02
	MONT	642	.08

Table 10—Attributes of site indices that have 4 possible values or that can be continuous between zero and 1.0

Index	Data source	Number of plot-years	Mean	Standard deviation	Minimum value	Maximum value
SLOPE	COLO	11	0.59	0.13	0.50	0.75
	NMEX	992	.51	.26	.25	1.00
	DAMAG	51	.59	.21	.25	1.00
	IDA	564	.63	.24	.25	1.00
	PNW	29	.25	0	.25	.25
	MONT	642	.45	.20	.25	1.00
	SAMP	19	.43	.23	.25	1.00
ELEV	NMEX	896	.87	.04	.79	1.00
	DAMAG	51	.92	.04	.81	1.00
	IDA	564	.78	.06	.56	1.00
	MONT	642	.87	.06	.75	1.00

Table 11—Attributes of indices[a] of outbreak proximity

Index	Data source	Number of plot-years	Mean	Standard deviation	Minimum value	Maximum value
$DST_{(n-1)}$	IDA	564	0.86	0.21	0	1.00
$SIZ_{(n-1)}$	WXBASE	176	.23	.28	0	.97
	IDA	564	.27	.15	0	.70
$SIZ_{(n)}$	WXBASE	198	.21	.27	0	.97
	IDA	564	.34	.22	0	.75

[a] The index equals the value of the attribute plus 0.5.

MART = index of March temperature (mean March temperature (in °F)/29.7).
Note: average mean March temperature = -1.3 °C.

MAY1 = index of May temperature (InMAY1 = 1 if mean May temperature < 5.7 °C; else = 0).

MAY2 = index of May temperature (InMAY2 = 1 if mean May temperature was between 5.7 and 6.8 °C; else = 0).

MAY3 = index of May temperature (InMAY3 = 1 if mean May temperature was between 6.8 and 8.8 °C; else = 0).

SUMT = index of temperature change from May to June (InSUMT = 1 if mean June temperature was within 0.8 °C of mean May temperature; else = 0).

PCP1 = index of May rainfall intensity (observed mean precipitation/rainy day in May)/ (average mean precipitation/rainy day in May, which = 0.89 cm).
Note: a rainy day is a day with ≥ 0.254 cm of precipitation.

PCP2 = index of May and June precipitation (InPCP2 = 1 if total precipitation for May and June was < 8.38; else = 0).

PCP3 = index of May, June, and July precipitation (InPCP3 = 1 if total precipitation for May, June, and July is between 10.5 and 14 cm; else = 0).

Attributes of the weather indices are summarized in table 13.

Table 12—Montana weather stations used in conjunction with the WXBASE data

Station	Elevation (ft)	Number of WXBASE plots that use weather indices from station
Bozeman Agricultural	4,856	2
Butte FAA	5,530	1
Darby	3,880	1
Deer Lodge	4,830	1
Divide 2 NW	5,406	1
Drummond FAA	4,240	1
Ennis	4,953	1
Helena WB	3,893	3
Lima	6,265	1
Lincoln Ranger	4,540	1
Livingston	4,485	2
Norris Madison	4,745	1
Ovando	4,100	1
Townsend	3,833	1
Virginia City	5,835	1
West Yellowstone	6,662	3
White Sulphur Springs	5,187	2
Wilsall	5,050	1

**3.2.5
Area, Treatment
History, and Year**

The following indices enabled me to examine the data for possible systematic differences among areas, long-term effects related to prior insecticide treatment, and systematic differences among years:

COLO =   index of area (COLO = 1 if plot is in COLO; else = 0).

PNW =   index of area (PNW = 1 if plot is in PNW; else = 0).

SAMP =   index of area (SAMP = 1 if plot is in SAMP; else = 0).

TRT =   index of insecticide treatment (InTRT = 1 if plot is in a treated block; else = 0).

$YR_i(i=1,n)$ =   index of year (InYR = 1 if year = year (i); else = 0).
         (In WXBASE, year 1 = 1959, year n = 1969
         In NMEX, year 1 = 1977, year n = 1980
         In DAMAG, year 1 = 1978, year n = 1982
         In IDA, year 1 = 1979, year n = 1982
         In MONT, year 1 = 1981, year n = 1983
         In OREG, year 1 = 1981, year n = 1988)

YRIDX =   index of year used with the OREG data (1981-88). (If year $\leq$ 1985 then InYRIDX = 1; else = 0).

Attributes of indices of treatment and year are summarized in table 14.

Table 13—Attributes of weather indices

Index	Total plot-years	Proportion of total plot-years where index=exp
Indices that have only two possible values (exp and 1):		
JANT	250	0.06
MAY1	250	.05
MAY2	250	.04
MAY3	250	.26
SUMT	250	.21
PCP2	250	.35

Index	Number of plot-years	Mean	Standard deviation	Minimum value	Maximum value
Indices that are continous:					
MART	249	0.98	0.24	0.49	1.47
PCP1	245	.96	.29	.53	2.47

Table 14—Attributes of indices of treatment and year

Index	Data source	Total plot-years	Proportion of total plot-years where index=exp
TRT	NMEX	992	0.49
	IDA	564	.41
	MONT	642	.66
YR1	NMEX	992	.25
	DAMAG	51	.33
	IDA	564	.04
	MONT	642	.33
YR2	NMEX	992	.25
	DAMAG	51	.33
	IDA	564	.25
	MONT	642	.33
YR3	NMEX	992	.25
	DAMAG	51	.33
	IDA	564	.37
	MONT	642	.33
YR4	NMEX	992	.25
	IDA	564	.33

3.2.6
Effects of Predators

In most of the PNW plots, whole-tree exclosures and sticky barriers were used to exclude birds, ants, or both groups from individual host trees about 9 m tall. (Campbell and others 1983b). The combined effect of birds and ants on survival across the interval from fourth instar to adults (E_{AB}) was estimated as the ratio between adult density (N_A) on trees protected from these predators and N_A on control trees (E_{AB} = [N_A on protected trees]/ [N_A on control trees]).

3.3
Analysis of Determination

The objective of these preliminary analyses was to identify the principal age-interval determinants of variation in egg-mass density ($\sigma^2 N_{M(n+1)}$). First, estimates of four densities (N_E, N_L, N_A, and N_M) were used to derive the following rates:

S_S = survival rate from eggs to fourth instar (N_L/N_E).
S_L = survival rate from fourth instar to emerging moth (N_A/N_L).
S_A = number of egg masses deposited per emerging moth (N_M/N_A).

Note: Each of the above rates represents the net influence of both on-site mortality-causing processes and interstand dispersal.

Preliminary, graphic examination showed that successive survival rates were often correlated. In such situations, the nonzero covariance terms shared between these variables influence the variation in $N_{M(n+1)}$. Further, the size and the sign of each covariance term is a precise description of the effect on $\sigma^2 N_{M(n+1)}$ of this varying together of the two independent variables. Thus, the variation in $N_{M(n+1)}$ was partitioned by a procedure proposed by Mott (1966). This procedure recognizes that an age-interval model represents an identity such that the variance in the dependent variable is exactly equal to the sum of the variances plus twice the sum of the covariances in the independent variables.

To obtain a basis for comparing among data sets, separate analyses of determination were performed on the data from IDA, MONT, NMEX, DAMAG, COLO, PNW, and OREG. In each instance, I used age-interval model (1), as follows:

$$\sigma^2 \ln N_M = \sigma^2 \ln N_E + \sigma^2 \ln S_S + \sigma^2 \ln S_L + \sigma^2 \ln S_A + 2[\text{cov.}\ln N_E \cdot \ln S_S \\ + \text{cov.}\ln N_E \cdot \ln S_L + \text{cov.}\ln N_E \cdot \ln S_A + \text{cov.}\ln S_S \cdot \ln S_L \\ + \text{cov.}\ln S_S \cdot \ln S_A + \text{cov.}\ln S_L \cdot \ln S_A] . \tag{1}$$

3.4
Formulating the Statistical Models

The analytical focus of this study was to develop one or more equations that relate variation in five dependent variables [EG, N_L, N_A, N_M, and DEF] to variation in preceding budworm density and other attributes of the budworm life system.

For several reasons, I decided to base the statistical models I would test on the assumption that each successive budworm density (and defoliation) reflects the mathematical product of some preceding budworm density and a subset of mutually interacting environmental attributes. First, in a persistent budworm population, each successive budworm density (as well as defoliation) is obviously a product of some prior density. Second, for many species, relations between that species and habitat attributes are commonly described in intuitively product terms such as "this habitat is twice as good" (for some species we value), or "that habitat is only half as bad" (for some species we deem a pest). Third, in developing a model that uses site and stand attributes to generate "...an index of the relative susceptibility of a given stand to budworm," Wulf and Carlson (1985) calculated their index as the product of several interacting values. That index "...has been field-tested...and appears to perform reasonably well." Consequently, for each of the five dependent variables, the equations that were developed have the general form:

$$Y_i = exp^a \cdot N_{(t-1)}{}^{b_1} \cdot X_1{}^{b_2} \cdot X_2{}^{b_3} \cdots X_n{}^{b_{(n+1)}} , \tag{2}$$

where

Y$_i$ is dependent variable i;
         the parameter a is derived from equation (3);
exp   is the base for natural logarithms;
N$_{(t-1)}$ is a preceding budworm density;
X$_i$ represents some attribute or index of the budworm life system; and
b$_i$ is the parameter that describes the relation between X$_i$ and Y$_i$.

To derive estimates of the parameters in model (2), the variables in the model were transformed to their natural logarithms. These transformations produced additive linear model (3):

$$lnY = a + b_1 lnN_{(t-1)} + b_2 lnX_1 + b_3 lnX_2 + ... + b_{(n+1)} lnX_n . \tag{3}$$

Log-scale predictions from model (3) are unbiased estimates, and the error terms are additive in the log scale. Estimates of lnY that are transformed back to the original scale, however, represent the geometric mean on the original scale. I used a procedure described in Baskerville (1972) to correct the intercept (a) for the difference between the expected geometric and arithmetic mean value of Y.

3.4.1
Model Subsets

Because I was uncertain about causal pathways, the same subsets of independent variables were tested repeatedly in several regression models. To minimize repetition in following sections, several of these subsets are described below.

3.4.1.1 The COLO, PNW, and SAMP studies—Indices of all site and stand attributes except elevation were derived for the plots in COLO, PNW, and SAMP. To facilitate direct comparisons among the data sets representing these studies, these three relatively small data sets were combined. Subsequently, the following subset (4) was used to represent site and stand attributes in these three studies:

$$[b_1 lnSLOPE + b_2 lnSASP + b_3 lnWASP + b_4 lnWET + b_5 lnPROD$$
$$+ b_6 lnDOUG + b_7 lnTRUE + b_8 lnSPR + b_9 lnAGE + b_{10} lnVCD$$
$$+ b_{11} lnSTK + b_{12} lnHISH + b_{13} COLO + b_{14} PNW + b_{15} SAMP$$
$$+ b_{16}(lnSLOPE \cdot COLO) + b_{17}(lnSLOPE \cdot PNW) + b_{18}(lnSLOPE \cdot SAMP)$$
$$+ b_{19}(lnSASP \cdot COLO) + b_{20}(lnSASP \cdot PNW) + b_{21}(lnSASP \cdot SAMP)$$
$$+ b_{22}(lnWASP \cdot COLO) + b_{23}(lnWASP \cdot PNW) + b_{24}(lnWASP \cdot SAMP)$$
$$+ b_{25}(lnWET \cdot COLO) + b_{26}(lnWET \cdot PNW) + b_{27}(lnWET \cdot SAMP)$$
$$+ b_{28}(lnPROD \cdot COLO) + b_{29}(lnPROD \cdot PNW) + b_{30}(lnPROD \cdot SAMP)$$
$$+ b_{31}(lnDOUG \cdot COLO) + b_{32}(lnDOUG \cdot PNW) + b_{33}(lnDOUG \cdot SAMP)$$
$$+ b_{34}(lnTRUE \cdot COLO) + b_{35}(lnTRUE \cdot PNW) + b_{36}(lnTRUE \cdot SAMP)$$
$$+ b_{37}(lnSPR \cdot COLO) + b_{38}(lnSPR \cdot PNW) + b_{39}(lnSPR \cdot SAMP)$$
$$+ b_{40}(lnAGE \cdot COLO) + b_{41}(lnAGE \cdot PNW) + b_{42}(lnAGE \cdot SAMP)$$
$$+ b_{43}(lnVCD \cdot COLO) + b_{44}(lnVCD \cdot PNW) + b_{45}(lnVCD \cdot SAMP)$$
$$+ b_{46}(lnSTK \cdot COLO) + b_{47}(lnSTK \cdot PNW) + b_{48}(lnSTK \cdot SAMP)$$
$$+ b_{49}(lnHISH \cdot COLO) + b_{50}(lnHISH \cdot PNW) + b_{51}(lnHISH \cdot SAMP)] . \tag{4}$$

3.4.1.2 The DAMAG project—Indices of all site and stand attributes (including elevation) together with year indices were derived for the plots in DAMAG. For this project, the following subset (5) was used to represent these attributes:

$$[b_1 \text{lnELEV} + b_2 \text{lnEL1} + b_3 \text{lnEL2} + b_4 \text{lnEL3} + b_5 \text{lnEL4} + b_6 \text{lnEL5}$$
$$+ b_7 \text{lnSLOPE} + b_8 \text{lnSASP} + b_9 \text{lnWASP} + b_{10} \text{lnWET} + b_{11} \text{lnPROD}$$
$$+ b_{12} \text{lnDOUG} + b_{13} \text{lnTRUE} + b_{14} \text{lnSPR} + b_{15} \text{lnAGE} + b_{16} \text{lnVCD}$$
$$+ b_{17} \text{lnSTK} + b_{18} \text{lnHISH} + b_{19} \text{lnYR2} + b_{20} \text{lnYR3} + b_{21} \text{lnYR4} + b_{22} \text{lnYR5}] . \quad (5)$$

3.4.1.3 The IDA, MONT, and NMEX projects—Variables in this subset include indices for treatment history and indices to identify differences in budworm-forest relations across a wide range in density. This subset (6) is as follows:

$$[b_1 \text{lnELEV} + b_2 \text{lnEL1} + b_3 \text{lnEL2} + b_4 \text{lnEL3} + b_5 \text{lnEL4} + b_6 \text{lnEL5}$$
$$+ b_7 \text{lnSLOPE} + b_8 (\text{lnSLOPE} \cdot \text{LO}) + b_9 (\text{lnSLOPE} \cdot \text{MED})$$
$$+ b_{10} (\text{lnSLOPE} \cdot \text{HI}) + b_{11} \text{lnSASP} + b_{12} (\text{lnSASP} \cdot \text{LO})$$
$$+ b_{13} (\text{lnSASP} \cdot \text{MED}) + b_{14} (\text{lnSASP} \cdot \text{HI}) + b_{15} \text{lnWASP}$$
$$+ b_{16} (\text{lnWASP} \cdot \text{LO}) + b_{17} (\text{lnWASP} \cdot \text{MED}) + b_{18} (\text{lnWASP} \cdot \text{HI})$$
$$+ b_{19} \text{lnWET} + b_{20} (\text{lnWET} \cdot \text{LO}) + b_{21} (\text{lnWET} \cdot \text{MED}) + b_{22} (\text{lnWET} \cdot \text{HI})$$
$$+ b_{23} \text{lnPROD} + b_{24} (\text{lnPROD} \cdot \text{LO}) + b_{25} (\text{lnPROD} \cdot \text{MED})$$
$$+ b_{26} (\text{lnPROD} \cdot \text{HI}) + b_{27} \text{lnDOUG} + b_{28} (\text{lnDOUG} \cdot \text{LO})$$
$$+ b_{29} (\text{lnDOUG} \cdot \text{MED}) + b_{30} (\text{lnDOUG} \cdot \text{HI}) + b_{31} \text{lnTRUE}$$
$$+ b_{32} (\text{lnTRUE} \cdot \text{LO}) + b_{33} (\text{lnTRUE} \cdot \text{MED}) + b_{34} (\text{lnTRUE} \cdot \text{HI})$$
$$+ b_{35} \text{lnSPR} + b_{36} (\text{lnSPR} \cdot \text{LO}) + b_{37} (\text{lnSPR} \cdot \text{MED}) + b_{38} (\text{lnSPR} \cdot \text{HI})$$
$$+ b_{39} \text{lnAGE} + b_{40} (\text{lnAGE} \cdot \text{LO}) + b_{41} (\text{lnAGE} \cdot \text{MED}) + b_{42} (\text{lnAGE} \cdot \text{HI})$$
$$+ b_{43} \text{lnVCD} + b_{44} (\text{lnVCD} \cdot \text{LO}) + b_{45} (\text{lnVCD} \cdot \text{MED}) + b_{46} (\text{lnVCD} \cdot \text{HI})$$
$$+ b_{47} \text{lnSTK} + b_{48} (\text{lnSTK} \cdot \text{LO}) + b_{49} (\text{lnSTK} \cdot \text{MED}) + b_{50} (\text{lnSTK} \cdot \text{HI})$$
$$+ b_{51} \text{lnHISH} + b_{52} (\text{lnHISH} \cdot \text{LO}) + b_{53} (\text{lnHISH} \cdot \text{MED})$$
$$+ b_{54} (\text{lnHISH} \cdot \text{HI}) + b_{55} \text{lnYR2} + b_{56} \text{lnYR3} + b_{57} \text{lnTRT}$$
$$+ b_{58} (\text{lnTRT} \cdot \text{LO}) + b_{59} (\text{lnTRT} \cdot \text{MED}) + b_{60} (\text{lnTRT} \cdot \text{HI})] . \quad (6)$$

**3.4.2
Projecting Eggs
per Mass**

3.4.2.1 Density-dependence—Miller (1957) found that the mean number of eggs per mass (EG) in the eastern budworm was 2.7 eggs higher in light than in severe infestations. Similarly, Harris (1963) reported that moths of a conifer-eating budworm species with a 2-year life cycle in British Columbia may have been incapable of laying a large number of eggs per mass in populations where defoliation had been severe. Across a lower density range, however, Campbell and others (1984b) showed that the number of eggs in western budworm egg masses increases as defoliation increases from none to about 50 percent.

Collectively, the above results suggest that EG might be a quadratic function of egg-mass density (N_M), as specified by equation (7):

$$EG = a + b_1 N_M + b_2 N_M^2 . \quad (7)$$

In this equation, the parameter a represents EG as N_M approaches zero. The term b_1N_M is a positive density-dependent function that relates increases in EG to changes in N_M. The term $b_2N_M^2$ represents the increasingly inverse density dependence of EG on N_M as N_M rises.

3.4.2.2 Using MONT—Except for a few observations from PNW, data from the first and second years of the MONT Project provided the only direct estimates of eggs per mass (EG). Graphic examination of these data suggested a nondeclining relation between egg-mass density (N_M) and EG. To test for possible influences of both N_M and other environmental components on EG, regression model (8) was tested:

$$lnEG = a + [subset (6)] + b_{61}lnN_M + b_{62}lnYR1 + b_{63}(lnYR1 \cdot lnN_M)$$
$$+ b_{64}(lnYR2 \cdot lnN_M) . \tag{8}$$

Unfortunately, any relations found in MONT between EG and environmental attributes other than N_M may be unique to these particular data. If so, they probably would be inappropriate for use in another area without further testing and calibration. For this reason, equation (7) also was tested as a regression model, as a way to derive estimates of EG in places where direct estimates of this variable are lacking.

3.4.3 Projecting Fourth Instars

3.4.3.1 Density dependence—For eastern budworm populations in New Brunswick, Mott (1963a) showed that survival of young larvae is inversely correlated with population density. Among these populations, this relation was most noticeable across relatively low densities. Survival from eggs to fourth instars was also a decreasing function of N_E among western budworm populations. Here, however, this relation was most evident above a threshold somewhere between 500 and 1,000 eggs per m^2 (Campbell 1987).

Together, the above results suggest that N_L in the western budworm might consistently increase across a wide range of preceding N_E but at a decreasing (density-dependent) rate. A commonly accepted equation to describe this relation (Varley and others 1973) is as follows (9):

$$N_L = aN_E^b . \tag{9}$$

Here, the parameter a represents both the value of N_L when N_E is 1 and a multiplier for the term N_E^b. The term N_E^b represents the change in N_L as N_E increases.

3.4.3.2 Using IDA(1)—Because they include two indices of suspected interstand influences (DST and SIZ), the IDA data provide an opportunity to evaluate both on-site attributes and these influences. Consequently, the following regression model (10) was tested:

$$lnN_L = a + [subset (6)] + b_{61}lnN_E + b_{62}lnYR4 + b_{63}(lnYR2 \cdot lnN_E)$$
$$+ b_{64}(lnYR3 \cdot lnN_E) + b_{65}(lnYR4 \cdot lnN_E) + b_{66}lnDST_{(n-1)}$$
$$+ b_{67}(lnDST_{(n-1)} \cdot LO) + b_{68}(lnDST_{(n-1)} \cdot MED) + b_{69}(lnDST_{(n-1)} \cdot HI)$$
$$+ b_{70}lnSIZ_{(n-1)} + b_{71}(lnSIZ_{(n-1)} \cdot lnYR2) + b_{72}(lnSIZ_{(n-1)} \cdot lnYR3)$$
$$+ b_{73}(lnSIZ_{(n-1)} \cdot lnYR4) . \tag{10}$$

3.4.3.3 Using IDA(2), MONT, and NMEX—The only difference between models tested against MONT and those tested against IDA and NMEX is induced by the fact that the former data set spans three years and the latter ones span four. Here are the regression models (11 and 12):

For MONT:
$$\ln N_L = a + [\text{subset (6)}] + b_{61} \ln N_E + b_{62}(\ln N_E \cdot \ln YR2) + b_{63}(\ln N_E \cdot \ln YR3) . \quad (11)$$

For IDA(2) and NMEX:
$$\ln N_L = [\text{model (11)}] + b_{64} \ln YR4 + b_{65}(\ln N_E \cdot \ln YR4) . \quad (12)$$

3.4.3.4 Using DAMAG—Regression model (13) was used to evaluate relations between N_L and environmental attributes in DAMAG:

$$\ln N_L = a + [\text{subset (5)}] + b_{23} \ln N_E + b_{24}(\ln N_E \cdot \ln YR2) + b_{25}(\ln N_E \cdot \ln YR3)$$
$$+ b_{26}(\ln N_E \cdot \ln YR4) + b_{27}(\ln N_E \cdot \ln YR5) . \quad (13)$$

3.4.3.5 Using COLO, PNW, and SAMP—I used a regression model (14) to evaluate relations between N_L and environmental attributes in COLO, PNW, and SAMP.

$$\ln N_L = a + [\text{subset (4)}] + b_{52} \ln N_E + b_{53}(\ln N_E \cdot COLO) + b_{54}(\ln N_E \cdot PNW)$$
$$+ b_{55}(\ln N_E \cdot SAMP) . \quad (14)$$

3.4.3.6 Using OREG—Among the various projects, the New Mexico Damage Assessment (DAMAG) and the Oregon Study (OREG) provide the only data that document changes in density from the approximate beginning of an extended outbreak. Regression model (15) was used to evaluate the OREG data for possible systematic year-to-year changes in budworm survival, as follows:

$$\ln S_S = a + b_1 \ln N_E + b_2 \ln YRIDX . \quad (15)$$

3.4.3.7 Using WXBASE—All but one of the weather indices that proved to be relevant were derived from records of weather phenomena that occur between January 1st and the following June 30th. For this reason, N_L would be an excellent dependent variable against which to test these data. Unfortunately, successive egg-mass densities and defoliation were the only variables estimated during this project. For this reason, I had to use egg density at the start of year (n+1) as the dependent variable in this analysis. Thus, the principal regression model used to evaluate relations between weather indices and the budworm (16) is as follows:

$$\ln N_{E(n+1)} = a + b_1 \ln N_{E(n)} + b_2 \ln JANT + b_3 \ln MART + b_4 \ln MAY1 + b_5 \ln MAY2$$
$$+ b_6 \ln MAY3 + b_7 \ln PCP1 + b_8 \ln SUMT + b_9 \ln PCP2 . \quad (16)$$

3.4.4 Projecting Defoliation

3.4.4.1 Density dependence—Equation (17) seemed appropriate to quantify the obvious density-dependent relation between fourth-instar density and defoliation of current-year foliage (DEF):

$$DEF = aN_L^b . \quad (17)$$

Here, the parameter a represents defoliation when on-site budworm density is one fourth instar per m². The term N_L^b represents the increase in defoliation as N_L increases.

3.4.4.2 Using IDA, MONT, and NMEX—For these data sets, I tested either regression model (18) or (19):

For MONT:

$$\ln\text{DEF} = a + [\text{subset (6)}] + b_{61}\ln N_L + b_{62}(\ln N_L \cdot \ln\text{YR2})$$
$$+ b_{63}(\ln N_L \cdot \ln\text{YR3}) . \tag{18}$$

For IDA and NMEX:

$$\ln\text{DEF} = [\text{model (18)}] + b_{64}\ln\text{YR4} + b_{65}(\ln N_L \cdot \ln\text{YR4}) . \tag{19}$$

3.4.4.3 Using DAMAG—Regression model (20) was used to evaluate these data:

$$\ln\text{DEF} = a + [\text{subset (5)}] + b_{23}\ln N_L + b_{24}(\ln N_L \cdot \ln\text{YR2})$$
$$+ b_{25}(\ln N_L \cdot \ln\text{YR3}) + b_{26}(\ln N_L \cdot \ln\text{YR4}) + b_{27}(\ln N_L \cdot \ln\text{YR5}) . \tag{20}$$

3.4.4.4 Using WXBASE—Data from this 11-year study provided an opportunity to evaluate year-to-year patterns in defoliation. The regression model tested (21) was:

$$\ln\text{DEF}_{(n)} = a + b_1\ln N_{M(n-1)} + b_2\ln\text{DEF}_{(n-1)} . \tag{21}$$

3.4.4.5 Defoliation of Douglas-fir versus white fir—Parker and others (1979) reported more defoliation on white fir than on nearby Douglas-fir in NMEX. Because the equations developed for this project are based exclusively on samples drawn from Douglas-fir, I decided to investigate the possibility of using defoliation of Douglas-fir to project defoliation of the white fir. Consequently, the relevant NMEX data were used to test the following zero-based model (22):

$$\text{Defol}_{(white)} = 100 - a\,[100 - \text{Defol}_{(Doug)}] + b\,[100 - \text{Defol}_{(Doug)}]^2 , \tag{22}$$

where

$\text{Defol}_{(white)}$ = percent defoliation of current-year foliage on white fir; and
$\text{Defol}_{(Doug)}$ = percent defoliation of current-year foliage on Douglas-fir.

3.4.5 Projecting Emerging Moths

3.4.5.1 Density dependence—For densities between about 1 and 30 fourth instars per m^2, Campbell (1987) showed a positive correlation between N_L and survival from fourth instars to residual pupae. Above and below that range, the data were too sparse to discern any underlying relation.

At extremely high late-instar densities, a larval population will inevitably exhaust its food supply, with ensuing population decline. For example, Watt (1963) showed that late-instar survival decreased among eastern budworm populations in New Brunswick as N_L increased beyond about 140 per m^2.

To ensure the ability to project the dome-shaped survival curve that would result from population declines, I chose equation (23), as follows:

$$N_A = aN_L^{b_1}(1 - b_2N_L). \tag{23}$$

In this equation, which is similar to a stock-recruitment relation described by Shepherd (1982), the parameters a and b_1 are similar to those in equations (9) and (17), and the term $(1 - b_2N_L)$ defines both negative density dependence and the density at which survivorship can be expected to fall to zero.

3.4.5.2 Using COLO, PNW, and SAMP—The regression model described in this

section uses data that represent combined observations from COLO (11), PNW (29), and SAMP (19). Densities of both residual pupae (N_P) and emerging moths (N_A) were estimated for the populations in both COLO and PNW. In SAMP, however, only N_P was estimated. For this reason, the model for these data specifies N_P, rather than N_A, as the dependent variable. Fortunately, in places where the survival rate from N_P to N_A has been estimated, this rate has usually been close to constant. For example, Campbell and others (1984a) found an average survival rate of 0.9 (range, 0.82 to 0.93) for this interval among populations in Idaho.

To derive estimates of the parameters specified in (23), the analysis was performed in two steps. First, N_P was regressed against both N_L and N_L^2 in a zero-based model (24):

$$N_P = b_1 N_L + b_2 N_L^2 . \tag{24}$$

Second, the residual variation in $\ln N_P$ [$\ln(N_P/(b_1 N_L + b_2 N_L^2))$] was examined as a function of $\ln N_L$ and other environmental attributes by using regression model (25), as follows:

$$\ln[N_P/(b_1 N_L + b_2 N_L^2)] = a + [\text{subset (4)}] + b_{52}\ln N_L . \tag{25}$$

3.4.5.3 Using OREG—Densities of emerging moths (N_A) representing 47 plot-years in OREG were regressed against both N_L and N_L^2, by using a zero-based model (26):

$$N_A = b_1 N_L + b_2 N_L^2 . \tag{26}$$

As before, the residual variation in $\ln N_A$ {$\ln[N_A/(b_1 N_L + b_2 N_L^2)]$} was examined as a function of $\ln N_L$ and other attributes. Here, I used regression model (27), as follows:

$$\ln[N_A/(b_1 N_L + b_2 N_L^2)] = a + b_1\ln N_L + b_2\ln \text{YRIDX} . \tag{27}$$

**3.4.6
Projecting Egg Masses**

3.4.6.1 Density dependence—Campbell and others (1983a) noted that western budworm egg densities in the Pacific Northwest were sometimes greater than the ability of emerging moths to produce eggs. These results, together with preliminary graphic examination of the IDA data, suggested that the density of new egg masses (N_M) may increase across the range of N_A, but at a declining rate. This relation could be described by equation (28), as follows:

$$N_M = a N_A^b . \tag{28}$$

The parameters in this equation serve purposes equivalent to those in (9) and (17).

3.4.6.2 Using IDA(1)—For this data set, I tested regression model (29), as follows:

$$\begin{aligned}
\ln N_M = {} & a + [\text{subset (6)}] + b_{61}\ln N_A + b_{62}\ln \text{YR4} \\
& + b_{63}(\ln N_A \cdot \ln \text{YR2}) + b_{64}(\ln N_A \cdot \ln \text{YR3}) \\
& + b_{65}(\ln N_A \cdot \ln \text{YR4}) + b_{66}\ln \text{DST}_{(n)} \\
& + b_{67}(\ln \text{DST}_{(n)} \cdot \text{LO}) + b_{68}(\ln \text{DST}_{(n)} \cdot \text{MED}) \\
& + b_{69}(\ln \text{DST}_{(n)} \cdot \text{HI}) + b_{70}\ln \text{SIZ}_{(n)} \\
& + b_{71}(\ln \text{SIZ}_{(n)} \cdot \ln \text{YR2}) + b_{72}(\ln \text{SIZ}_{(n)} \cdot \ln \text{YR3}) \\
& + b_{73}(\ln \text{SIZ}_{(n)} \cdot \ln \text{YR4}) . \tag{29}
\end{aligned}$$

3.4.6.3 Using IDA(2), MONT, and NMEX—For these data sets (IDA, MONT, and NMEX), I tested regression models (30) and (31):

For MONT:
$$lnN_M = a + [subset (6)] + b_{61}lnN_A + b_{62}(lnN_A \cdot lnYR2) + b_{63}(lnN_A \cdot lnYR3) . (30)$$

For IDA(2) and NMEX:
$$lnN_M = [model (30)] + b_{64}lnYR4 + b_{65}(lnN_A \cdot lnYR4) . \tag{31}$$

3.4.6.4 Using DAMAG—I evaluated these data by using model (32):

$$lnN_M = a + [subset (5)] + b_{23}lnN_A + b_{24}(lnN_A \cdot lnYR2) + b_{25}(lnN_A \cdot lnYR3)$$
$$+ b_{26}(lnN_A \cdot lnYR4) + b_{27}(lnN_A \cdot lnYR5) . \tag{32}$$

3.4.6.5 Using COLO and PNW—Observations were made on both N_A and subsequent N_M in both COLO and PNW (but not in SAMP). The following regression model (33) was tested against the combined COLO-PNW data:

$$lnN_M = a + b_1lnSLOPE + b_2lnSASP + B_3lnWASP + b_4lnWET$$
$$+ b_5lnPROD + b_6lnDOUG + b_7lnTRUE + b_8lnSPR$$
$$+ b_9lnAGE + b_{10}lnVCD + b_{11}lnSTK + b_{12}lnHISH$$
$$+ b_{13}COLO + b_{14}PNW + b_{15}lnN_A + b_{16}(lnN_A \cdot COLO)$$
$$+ b_{17}(lnN_A \cdot PNW) + b_{18}(lnSLOPE \cdot COLO)$$
$$+ b_{19}(lnSLOPE \cdot PNW) + b_{20}(lnSASP \cdot COLO)$$
$$+ b_{21}(lnSASP \cdot PNW) + b_{22}(lnWASP \cdot COLO)$$
$$+ b_{23}(lnWASP \cdot PNW) + b_{24}(lnWET \cdot COLO)$$
$$+ b_{25}(lnWET \cdot PNW) + b_{26}(lnPROD \cdot COLO)$$
$$+ b_{27}(lnPROD \cdot PNW) + b_{28}(lnDOUG \cdot COLO)$$
$$+ b_{29}(lnDOUG \cdot PNW) + b_{30}(lnTRUE \cdot COLO)$$
$$+ b_{31}(lnTRUE \cdot PNW) + b_{32}(lnSPR \cdot COLO)$$
$$+ b_{33}(lnSPR \cdot PNW) + b_{34}(lnAGE \cdot COLO)$$
$$+ b_{35}(lnAGE \cdot PNW) + b_{36}(lnVCD \cdot COLO)$$
$$+ b_{37}(lnVCD \cdot PNW) + b_{38}(lnSTK \cdot COLO)$$
$$+ b_{39}(lnSTK \cdot PNW) + b_{40}(lnHISH \cdot COLO)$$
$$+ b_{41}(lnHISH \cdot PNW) . \tag{33}$$

3.4.6.6 Using OREG—Model (34) was used to evaluate density dependence and year-to-year differences between N_A and subsequent N_M in OREG:

$$lnN_M = a + b_1lnN_A + b_2lnYR1 + b_3lnYR2 + b_4lnYR3 + b_5lnYR4$$
$$+ b_6lnYR5 + b_7lnYR6 + b_8lnYR7 + b_9lnYR8 . \tag{34}$$

3.4.6.7 Using WXBASE—My objective with WXBASE was to test a regression model that would facilitate evaluation of relations between N_M and three environmental attributes: defoliation (DEF), precipitation from spring through midsummer (PCP3), and an index of outbreak size (SIZ). To reach this objective, I used the equation described in section 4.3.2.8 to calculate expected egg density ($N_{E(CALC)}$) as a function of preceding density and attributes of weather. Subsequently, lnN_M was examined as a function of $N_{E(CALC)}$ and SIZ by using model (35):

$$
\begin{aligned}
lnN_{M(n)} = \quad & a + b_1 lnN_{E(CALC)} + b_2 lnDEF + b_3 lnPCP3 + b_4 lnSIZ \\
& + b_5 (lnSIZ \cdot lnYR2) + b_6 (lnSIZ \cdot lnYR3) \\
& + b_7 (lnSIZ \cdot lnYR4) + b_8 (lnSIZ \cdot lnYR5) \\
& + b_9 (lnSIZ \cdot lnYR6) + b_{10} (lnSIZ \cdot lnYR7) \\
& + b_{11} (lnSIZ \cdot lnYR8) + b_{12} (lnSIZ \cdot lnYR9) \\
& + b_{13} (lnSIZ \cdot lnYR10) + b_{14} (lnSIZ \cdot lnYR11) . \quad\quad (35)
\end{aligned}
$$

3.5
Testing the Models and Examining Selected Relations

To test the regression models, I used a multiple regression technique called "maximum R^2 improvement" (MAXR). According to Ray (1982), the technique "...is considered superior to the stepwise technique and almost as good as all possible regressions....The difference between the stepwise technique and ....(MAXR) is that all switches are evaluated before any switch is made in the MAXR method."

For each analysis, the t-ratio of each variable and the associated degrees of freedom (d.f.) were used to decide whether to accept that variable. For acceptance in any given equation, each of the analyses that follow used a significance level of 0.05 for each variable, unless otherwise specified.

All analyses were performed on an IBM 3090/150, at the Syracuse University Computer Center, Syracuse, New York.

Consistently, the regression results summarized in the next chapter suggest that several dominant processes in the budworm life system are reflected by correlations between each dependent variable and a few key independent variables. In all models, each suspected key variable that was identified was significant in the multivariate analysis at $p = 0.005$, or better.

Both graphic and tabular methods were used to examine suspected key relations further. First, indices that can take only one of two (or a few) values (such as WET or AGE) were pooled by value, and means of the relevant dependent variable together with their standard errors, were calculated. Second, for continuous variables, such as prior density, graphic methods are used to identify and display univariate relations between the key independent variable and each selected dependent variable.

3.6
Simulating Changes Across a Generation

Equations that project both budworm densities (N_L, N_A, N_M, EG) and defoliation (DEF) as functions of environmental attributes are described in the following chapter. Several equations have been developed for each of the above dependent variables, and vastly different values of four variables (N_L, DEF, N_A, and N_M) are sometimes projected by different equations, from similar starting conditions.

To assist in deriving a realistic overview of budworm population dynamics, I used the empirically based equations in Chapter 4 to select a set of predictor variables that was often significant during outbreaks, and a second set that was significant during suboutbreaks. For each variable, I chose a parameter value that seemed to reflect an approximate average of the empirical results.

In Chapter 5, I will refer occasionally to projections from this generalized simulator.

4

Results

...the research has...brought us to realize how impotent we have been and still are to recognize and control all those forces affecting the abundance of any...species....
—From "The Ruffed Grouse: Life History, Propagation, Management" Gardiner Bump (1947)

4.1
Characteristics of the Data Base

4.1.1
Budworm Densities and Defoliation

Mean N_M ranged from 3.86 egg masses per m² (the average density found in IDA at the start of four successive budworm generations) to 35.99 egg masses per m² (the average found in MONT at the end of three generations). In individual plots, nonzero densities of N_M ranged from 0.08 to 245.7 (table 2).

Mean values of EG were very close in MONT and PNW (40.7 and 44.2), but estimates of EG in individual plots in MONT ranged from 6.4 to 76.2 (table 3). In the remaining projects, values of EG were calculated from observations on N_M (section 4.3.1).

Mean N_E ranged from 127.8 eggs per m² in IDA to 1,547.5 in MONT, but individual nonzero plot densities of N_E ranged from 2.2 to an astonishing 12,667.7 (table 3).

Mean N_L was lowest in NMEX, at 10.1 per m², and highest in SAMP, at 73.1 per m². In individual plots, nonzero values of N_L ranged from 0.05 to 166.5 per m² (table 4).

In several projects (IDA, MONT, NMEX, and DAMAG), values for the density of emerging moths (N_A) were calculated from observations on preceding N_L (section 4.6.1). Estimates of mean N_A were lowest in NMEX, at 2.0 per m², and highest in COLO at 11.5. In individual plots, estimates of N_A ranged from 0.001 to 21.7 per m² (table 5).

Data representing N_E, N_L, N_A, and N_M in the three largest projects (IDA, MONT, and NMEX) were pooled. For each budworm stage, the pooled data were stratified into three density categories (low, medium, and high) of about equal size. For each project area and budworm stage, I then calculated both mean density and the proportion of the total number of plot-years that were in the category (fig. 3). As shown by the figure, high densities of both eggs and subsequent egg masses were most frequent in MONT, but low densities of both eggs and subsequent egg masses were most common in IDA.

By the time the insects reached nominal fourth instar, the situation described above had changed. Here, high values of N_L were most common in IDA. This trend toward higher density in IDA continued as the insects passed from fourth instar to adults.

Mean percentage of defoliation of current-year foliage was lowest in NMEX, at 21.9 percent, and highest in DAMAG, at 69.9 percent. In individual plots, estimates of defoliation ranged from zero to 100 percent (table 6).

4.1.2
Survival Rates

Mean, minimum, and maximum rates for S_S, S_L, and S_A are shown for each project in table 15. Mean S_S ranged from a low of 0.018 in MONT to a high of 0.478 in IDA. In individual plots, S_S ranged from a low of 0.0003 in MONT to a high of 4.85 in IDA.

Mean S_L ranged from 0.127 in NMEX to 0.282 in COLO. The lowest value of S_L in an individual plot was 0.007, which was found in both PNW and OREG, but the maximum value was 0.76—again in PNW.
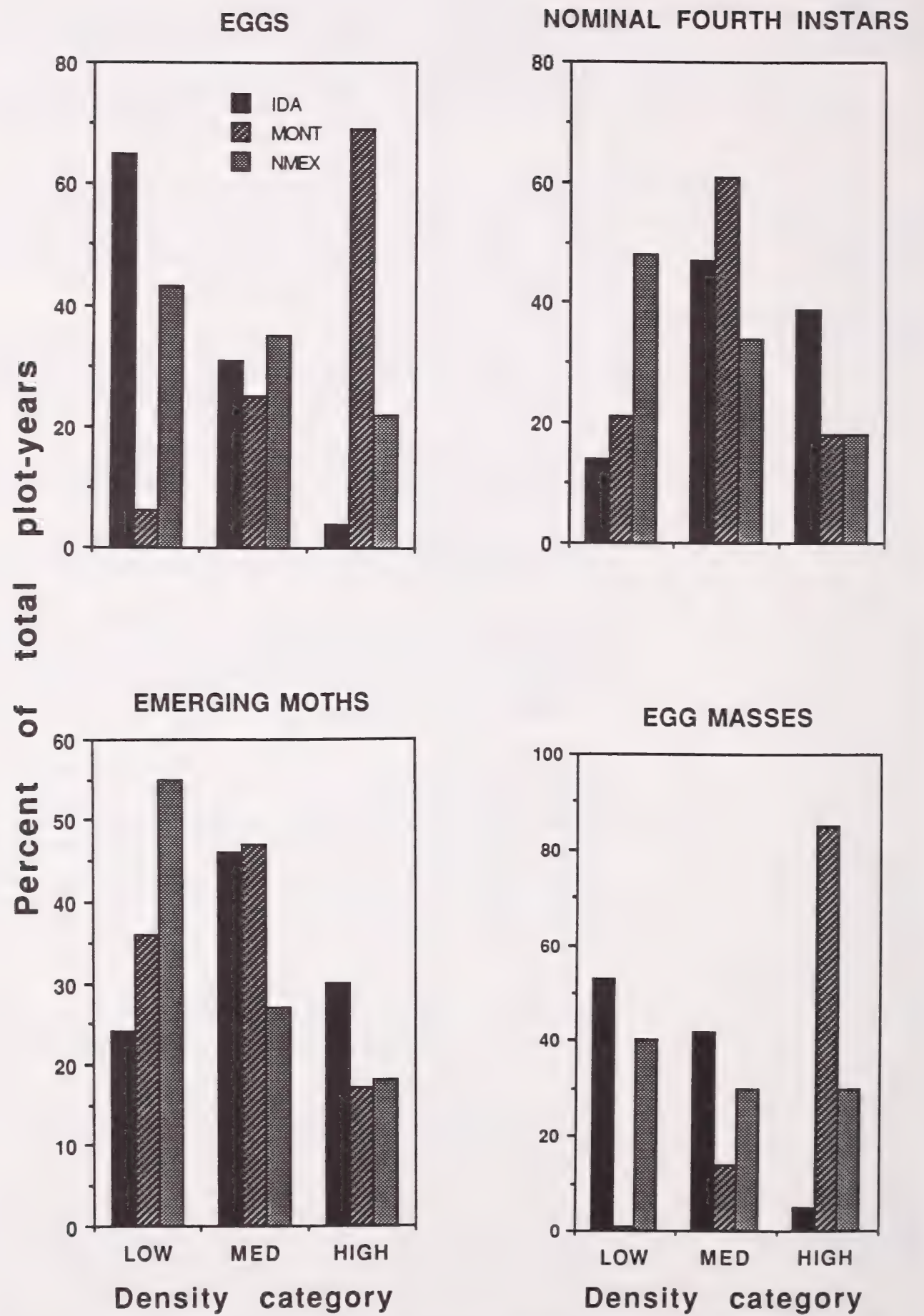
Figure 3—Percent of total plot-years where densities were categorized as low, intermediate, and high in IDA, MONT, and NMEX.

Table 15—Budworm survival rates, which represent the net influence of both onsite mortality processes and interstand dispersal

Survival rate	Data source	Number of plot-years	Mean	Standard deviation	Minimum value	Maximum value
S_S	COLO	11	0.197	0.122	0.055	0.49
	· NMEX	324	.072	.096	.001	1.05
	DAMAG	46	.109	.378	.006	2.41
	IDA	414	.478	.490	.004	4.85
	PNW	29	.116	.078	.017	.32
	MONT	428	.018	.032	.0003	.33
	OREG	47	.264	.361	.001	2.04
S_L	COLO	11	.282	.186	.104	.72
	NMEX	625	.127	.086	.016	.41
	DAMAG	51	.170	.213	.013	.74
	IDA	546	.143	.074	.020	.41
	PNW	29	.221	.199	.007	.76
	MONT	501	.144	.060	.026	.32
	OREG	47	.204	.161	.007	.63
	SAMP	19	.174	.120	.042	.43
S_A	COLO	11	10.12	5.11	3.20	19.1
	NMEX	357	29.52	75.64	.35	888.6
	DAMAG	51	70.86	274.61	1.70	1,811.1
	IDA	414	4.45	18.41	.01	345.0
	PNW	29	8.62	7.40	.78	29.9
	MONT	426	50.76	75.02	.09	758.5
	OREG	49	2.17	2.82	.04	16.4

Mean S_A ranged from a low of 2.17 in OREG to a high of 70.86 in DAMAG. Among individual plots, nonzero values of S_A ranged from a minimum of 0.01 in IDA to a spectacular 1,811.1 new egg masses per emerging moth in one of the plots in DAMAG.

As before, the data for each budworm stage in IDA, MONT, and NMEX, were stratified into low, medium, and high density categories, and survival rates were calculated for each project and category (fig. 4). In all three projects, mean S_S and S_A both decreased as density increased. Conversely, mean S_L increased as density increased.

4.1.3 Environmental Indices

Attributes of the environmental indices used are summarized in tables 7-14. Cursory examination of these summaries reveals that several attributes were not represented in some of the smaller data sets. For example, the three COLO plots (11 plot-years) were all classified as both fully stocked (InSTK always = 1), and having below average or average shrub density (InHISH always = 0) (table 7). Similarly, none of the 17 plots in DAMAG (51 plot-years) was classified as having a southern aspect (table 9).

Fortunately, each of the three largest projects (NMEX, IDA, and MONT) was represented by so many plots that a few plots in each project represented extreme values of nearly every index used in this study. Even among these three projects, however, very few plots were characterized by less than 50 percent of host foliage (Douglas-fir, true fir, and spruce) in the overstory. In MONT, the overstory in an average plot was overwhelmingly (98 percent) Douglas-fir.
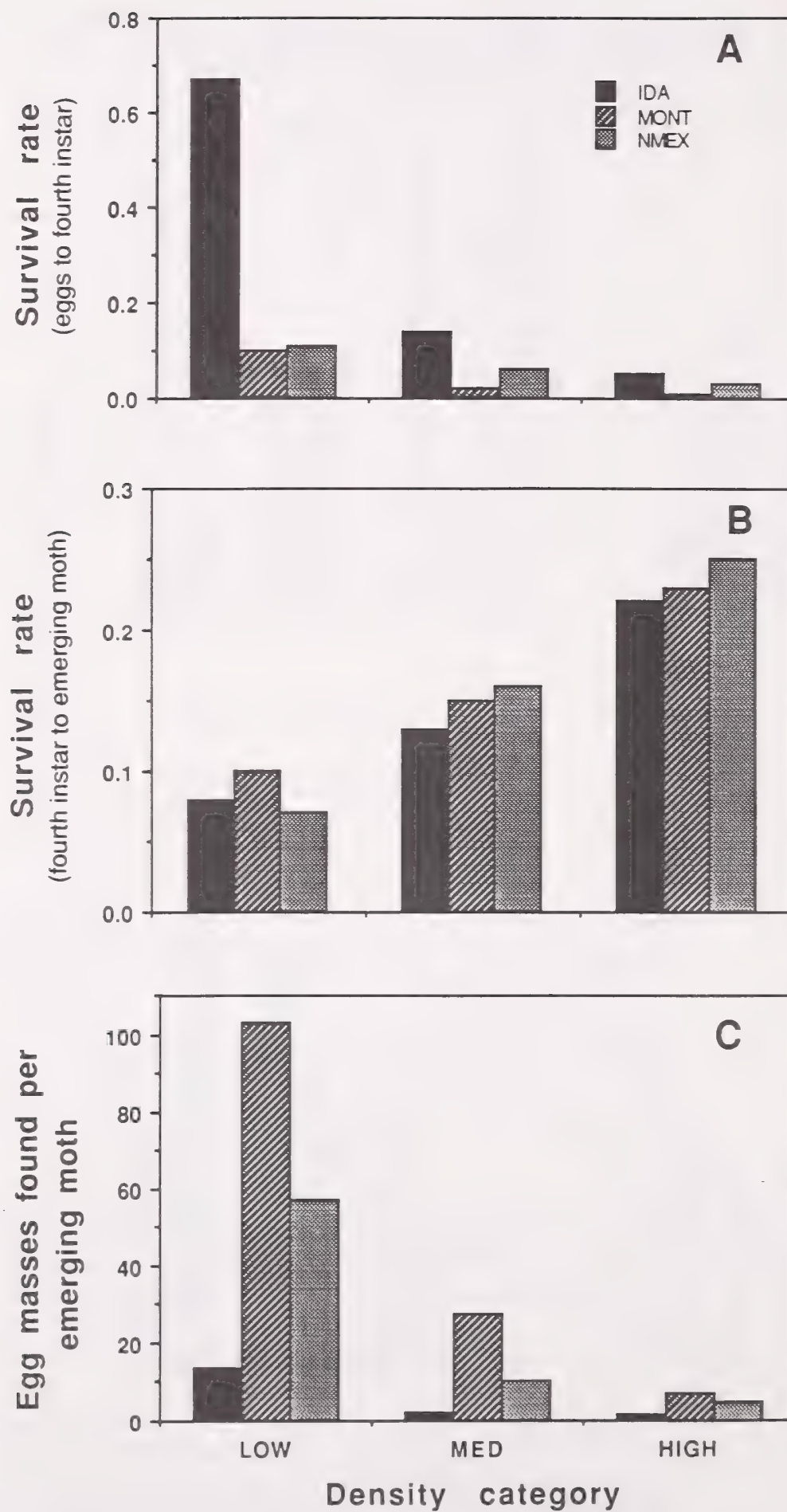
Figure 4—Mean survival rates in plots where densities were categorized as low, intermediate, and high in IDA, MONT, and NMEX: A, survival, eggs to fourth instar; B, survival, fourth instar to emerging moth; and C, egg masses found per emerging moth.

4.1.4
Life Tables

In all, I was able to derive 1,251 skeletal life tables for the western budworm, distributed as follows among the various studies: IDA, 414; MONT, 426; NMEX, 267; DAMAG, 63; COLO, 11; PNW, 29; and OREG, 41. Each life table includes an estimate of both eggs per mass (EG) at the start of the year and each of the following quantities per square meter of foliage:

$N_{M(n)}$ = egg masses at start of year n,
N_L = nominal fourth instars,
N_A = emerging adult moths, and
$N_{M(n+1)}$ = egg masses at the start of year (n+1).

All the above studies provided direct estimates of $N_{M(n)}$, N_L and $N_{M(n+1)}$. To complete these life tables for most of the studies, estimates of EG and N_A were derived by methods described in sections 4.3.1 and 4.6.1.

4.1.5
Analysis of Determination

Results of the analyses using model (1) are shown in table 16 for seven of the data sets (COLO, NMEX, DAMAG, IDA, PNW, MONT, and OREG). In each of these projects, large variances were found in both N_E and each of the three successive rates (S_S, S_L, and S_A), as compared to the subsequent variance in N_M. In two of these projects (DAMAG and MONT), variation in both S_S and S_A was much greater than the variation in subsequent N_M.

With few exceptions, covariances shared between pairs of variables made important contributions to variation in N_M. Compared with equivalent variance-covariance matrices for populations of the gypsy moth, *Lymantria dispar* (L.) (Campbell 1967), or even the jack pine budworm populations studied in the Lake States (Batzer and Jennings 1980, Foltz and others 1972), huge negative covariances occurred between successive survival rates in western budworm populations in DAMAG, IDA, and MONT. In every area, the net result of these covariances across the entire budworm generation was a diminution in subsequent variation in egg-mass density. Major patterns found in the various covariance terms are summarized below.

N_E and S_S—With one exception (the nonoutbreak populations in PNW), an inverse relation was found between N_E and S_S. This inverse relation made an important contribution by damping variation in ensuing density.

N_E and S_L—In general, N_E and S_L varied together. Consequently, the covariance shared between these variables magnified the direct influence of each of the individual terms. In COLO, unlike the other areas, an inverse relation was found between N_E and S_L. Undoubtedly, this inverse relation was a consequence of the high fourth-instar densities in that study.

N_E and S_A—With one exception (the outbreak in OREG), a negative covariance was found between N_E and S_A. Like the relation between N_E and S_S, this inverse relation served to dampen variation in subsequent density.

N_E and N_M—Except for the populations in COLO, N_E and N_M varied together. Commonly, the covariance between these two variables was about half as large as the variation in N_M. In COLO, unlike the other areas, high egg densities clearly tended to be followed by low egg-mass densities, and vice versa.

Table 16—Components of variance in $\ln N_M$, expressed as percentages of the total variance

Item	$\ln N_E$	$\ln S_S$	$\ln S_L$	S_A	$\ln N_M$
COLO, $\sigma^2 = 0.689$; N = 11					
$\ln N_E$	62.9	-53.2	-19.8	-32.3	-42.4
$\ln S_S$	--	57.1	8.0	27.6	39.5
$\ln S_L$	--	--	51.6	8.6	48.4
$\ln S_A$	--	--	--	56.6	54.5
$\ln N_M$	--	--	--	--	100.0
NMEX, $\sigma^2 = 1.777$; N = 267					
$\ln N_E$	87.3	-34.8	21.3	-16.3	57.5
$\ln S_S$	--	60.5	6.6	-31.5	.8
$\ln S_L$	--	--	20.1	-24.8	23.2
$\ln S_A$	--	--	--	91.1	18.5
$\ln N_M$	--	--	--	--	100.0
DAMAG, $\sigma^2 = 0.644$; N = 46					
$\ln N_E$	452.3	-290.9	51.2	-110.0	102.6
$\ln S_S$	--	233.7	-20.5	34.8	-42.9
$\ln S_L$	--	--	39.8	-45.2	25.3
$\ln S_A$	--	--	--	135.5	15.0
$\ln N_M$	--	--	--	--	100.0
IDA, $\sigma^2 = 1.601$; N = 414					
$\ln N_E$	147.1	-97.5	12.7	-20.7	41.6
$\ln S_S$	--	116.9	7.5	-22.3	4.6
$\ln S_L$	--	--	18.9	-21.4	17.8
$\ln S_A$	--	--	--	100.4	36.0
$\ln N_M$	--	--	--	--	100.0
PNW, $\sigma^2 = 2.300$; N = 29					
$\ln N_E$	58.0	4.3	22.7	-33.1	51.9
$\ln S_S$	--	21.7	8.8	-21.0	13.8
$\ln S_L$	--	--	67.1	-36.2	62.4
$\ln S_A$	--	--	--	62.2	-28.1
$\ln N_M$	--	--	--	--	100.0
MONT, $\sigma^2 = 0.535$; N = 426					
$\ln N_E$	289.5	-162.7	37.1	-118.8	45.1
$\ln S_S$	--	180.4	.2	-38.0	-20.1
$\ln S_L$	--	--	35.0	-66.1	6.1
$\ln S_A$	--	--	--	291.8	68.9
$\ln N_M$	--	--	--	--	100.0
OREG, $\sigma^2 = 2.115$; N = 41					
$\ln N_E$	55.4	-45.5	1.8	20.6	32.3
$\ln S_S$	--	85.5	18.3	-38.9	19.4
$\ln S_L$	--	--	49.5	-30.9	38.7
$\ln S_A$	--	--	--	58.8	9.5
$\ln N_M$	--	--	--	--	100.0

S_S **and** S_L—In general, the covariance shared between S_S and S_L made a relatively modest positive contribution to subsequent variation. Unlike the other areas, however, a negative covariance was found between these rates in DAMAG. As previously mentioned, the populations in DAMAG were undergoing a spectacular new outbreak at the time the observations were taken. As a consequence of this outbreak, S_S in DAMAG declined considerably after the first year of the study (equation 37). Possibly, the negative covariance between S_S and S_L in this area was an incidental attribute of this decline.

S_S **and** S_A—In general an inverse relation was found between S_S and S_A. In areas where this negative covariance occurred, it tended to reduce subsequent variation, particularly when coupled with the generally negative covariances between N_E and both S_S and S_A. Unlike the other areas S_S and S_A tended to increase together in both COLO and DAMAG.

S_S **and** N_M—Although variation in S_S was large, variation in the variable usually made a rather modest net contribution to variation in subsequent N_M. Clearly, the generally negative covariance terms between S_S and both N_E and S_A damped the large original variation in S_S. Unlike most of the other areas, S_S made a major net contribution to N_M in COLO. In this area, however, a positive covariance term was found between S_S and S_A.

S_L **and** S_A—Except in COLO, a negative covariance was found between S_L and S_A. Thus, the number of egg masses per emerging moth was usually correlated inversely with survival from fourth instar to adults. Again, this negative covariance tended to reduce variation in egg-mass density. Unlike the other areas, a modest positive covariance was found between S_L and S_A in COLO.

S_L **and** N_M—In every population set, variation in S_L and N_M tended to increase together. In several projects (COLO, PNW, and OREG), the net relation between these two variables made a particularly major contribution to variation in N_M. These results suggested that variation in S_L is particularly important during nonoutbreak periods (PNW), and that the role played by survival during this interval may decline during prolonged outbreaks, such as those in MONT and NMEX.

S_A **and** N_M—A highly variable relation was found between S_A and N_M. In the nonoutbreak PNW populations, this covariance was strongly negative. In the prolonged outbreak in MONT, however, it was strongly positive. At least during outbreaks, the relation between S_A and N_M showed a general, albeit highly variable, tendency to increase variation in N_M.

4.2 Projecting Eggs per Mass

For the MONT analyses, I used the 428 plot-years in the Montana B.t. Project (214 from 1981, and an equal number from 1982) that include observations on both egg-mass density (N_M) and eggs per mass (EG).

4.2.1 The Equations for MONT

Using Model (7)—Graphic examination revealed a close relation between N_M and EG. Regression model (7) provided a way to test this relation. The results of this test are summarized in equation (36), as follows:

$$EG = 27.1 + 0.545N_M - 0.00215N_M{}^2; (R^2 = 0.615) . \tag{36}$$

Using Model (8)—Regression model (8) was used to identify relations between lnEG and both lnN_M and other environmental attributes. In this test, 14 statistically significant variables were identified, and 3 of these 14 variables [lnN_M, lnYR2, and (lnWET · MED)] were associated with most of this same variation in lnEG (table 17). In the reduced model,

Table 17—Regression coefficients for estimating eggs per mass (lnEG), using model (8); data from MONT,   N = 428

Variable	Full model	Reduced model
Intercept[a]	3.122	2.894
lnN_M	.128	.206
$(lnN_M \cdot lnYR1)$	.110	
lnYR2	.630	.261
lnDEF	.146	
lnTRT	-.068	
$(lnTRT \cdot LO)$	.425	
lnEL5	-.121	
lnSLOPE	-.198	
$(lnWASP \cdot LO)$	-.531	
$(lnWET \cdot MED)$	.148	.130
lnDOUG	-.721	
$(lnAGE \cdot LO)$	1.102	
lnSTK	.049	
$(lnSTK \cdot LO)$	-.509	
R^2	.658	.578
RTMSE	.220	.242

[a] Intercept corrected for logarithmic bias.

each of these three variables is significant beyond $p = 0.001$. The order in which these variables entered the reduced model was:

Step	Variable	R^2
1	lnN_M	0.464
2	lnYR2	.567
3	$(lnWET \cdot MED)$	.578

**4.2.2
Relations Specified
by the Results**

4.2.2.1 Density dependence—Within each of two years, N_M and EG in MONT increased together across an extremely broad range. Even at extraordinarily high values of N_M, I found no indication that EG was beginning to decline (fig. 5). These results support but also greatly extend those of Campbell and others (1984b), which showed that average EG in western budworm increases as defoliation increases from none to moderate.

An estimated mean of 50.76 egg masses per emerging moth were deposited in MONT (table 15). This high ratio leaves no doubt that MONT was subjected to at least one massive inflight by adult moths. Consequently, the strong positive correlation between N_M and EG in MONT suggests that the ovipositional behavior of the female moths in these plots was stimulated by some factor or factors related to the presence and abundance of other moths, fresh egg masses, or other budworm activity. Both a possible causative process and certain implications arising from this finding are discussed further in section 5.2.2.4.
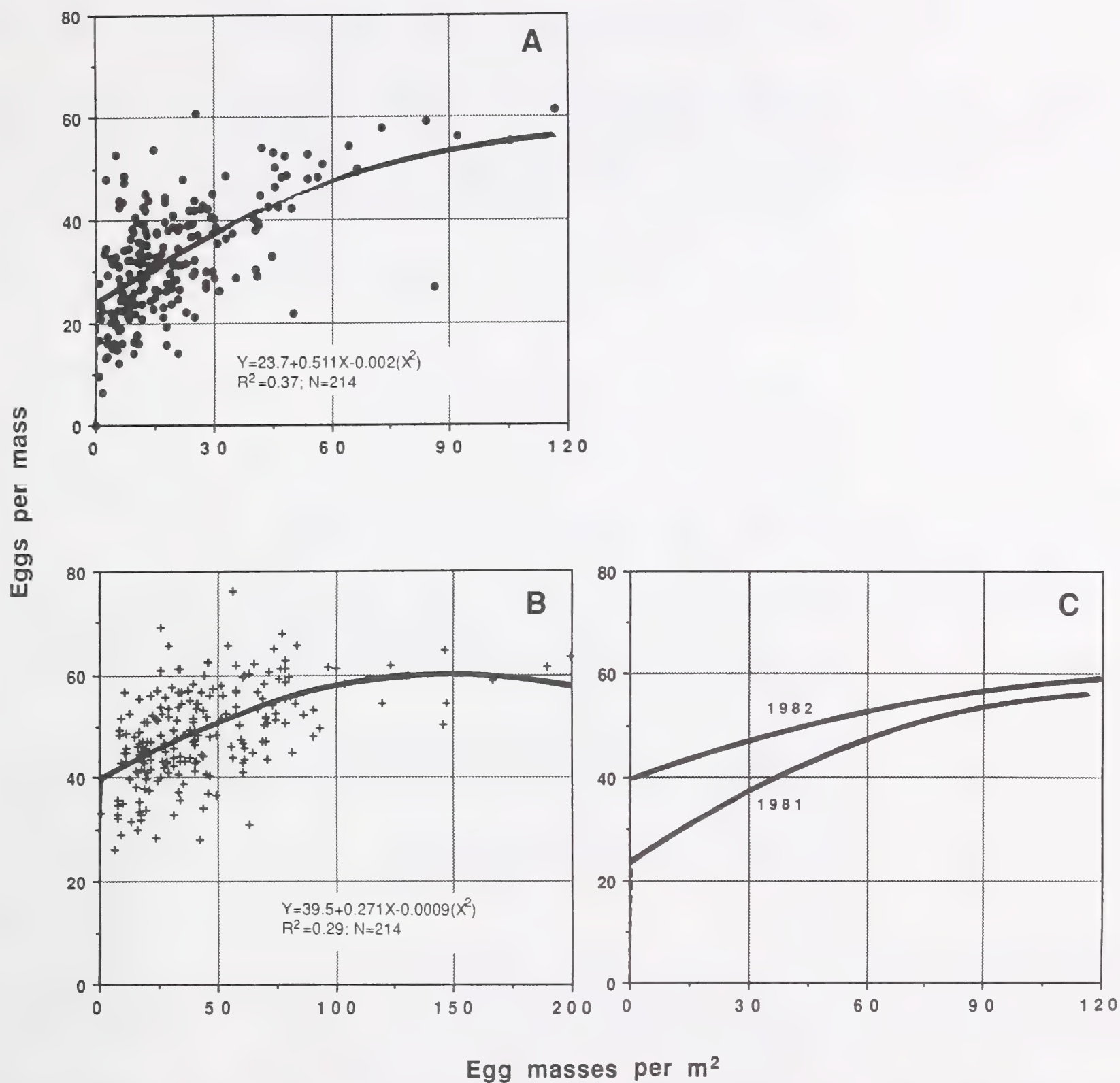
Figure 5—Egg-mass density and eggs per mass in MONT: A, 1981; B, 1982; C, comparison, 1981 and 1982.

4.2.2.2 Parameter stability across budworm density—Relations between EG and environmental attributes sometimes shifted dramatically as the index of density shifted from low (LO) to moderate (MED), or from MED to high (HI). For example, at most values of N_M, recent insecticide treatment was associated with slightly reduced values of EG. At low densities, however, values of EG were higher in the treated plots (table 17). In addition, several environmental attributes were only related to EG in one of the three

density strata. Some implications that arise from these and similar shifting relations across a range in budworm density are discussed in sections 5.2.7 and 5.3.1.

4.2.2.3 Differences across years—Estimates of EG were derived for each of the MONT plots in successive years (1981 and 1982). The relation between N_M and EG differed systematically between the two years (fig. 5). In comparison, Miller (1957) found that EG was slightly higher in light infestations of eastern budworms than in severe ones in New Brunswick. Subsequently, Miller (1963a) showed that eastern budworm fecundity is inversely related to both preceding larval density and defoliation history. In both eastern and western budworm, fecundity, which undoubtedly has some influence on EG, is known to be affected largely by the quantity and quality of food available to the preceding larvae (Blais 1952, Kirkbride and Wagner 1983).

Although generation-to-generation differences are probably universal in biological systems, the magnitude of the annual differences in MONT is surprising. With only two years of data as a base, speculating on possible causes of these systematic differences may be premature. Significantly, however, the area selected for the MONT project had been subjected to a budworm outbreak for several years before the project was initiated (Stipe and others 1983). Thus, the systematic differences in average EG between 1981 and 1982 were **not** related to a single defoliation event.

4.2.2.4 Influence of on-site defoliation—Defoliation and EG increased together in MONT (table 17). Like the relation between EG and N_M, this correlation was unexpected. As before (section 4.2.2.1), the relation between defoliation and EG suggests to me that the ovipositional behavior of these moths was stimulated by a factor or factors related to some recent budworm activity.

4.2.2.5 Influence of site—EG was higher in sites that rated wetter than average, at least when N_M was between 3.5 and 15 egg masses per m^2 (table 17). In this density range, mean values for EG were:

Plot category	Number of plot-years	Mean EG	Standard error
Wet	27	36.28	1.95
Other	87	30.18	1.09

Until validation data have been accumulated and analyzed, speculating on the underlying processes possibly causing the correlations between EG and plot wetness seems premature.

4.3 Projecting Fourth Instars

4.3.1 Calculating Egg Density

Although each project provided direct estimates of N_M, only three (COLO, MONT, and PNW) provided similar direct estimates of N_E. For the remaining projects, N_E was estimated as the product of N_M and values of EG that were derived from equation (36). These estimates of N_E were used in developing the equations described in this section.

4.3.2 The Equations

4.3.2.1 IDA(1)—For the IDA analyses, I used the 414 observations from the Idaho Control Project that included estimates of both N_E and subsequent N_L. Among the various data sets, IDA is the only one that includes indices of both the distance to visible defoliation

(DST) and outbreak size in the area surrounding each plot (SIZ). Variables that incorporate these indices are included in model (10).

When this model was tested, 11 statistically significant variables were associated with the variation in $\ln N_L$. Five of these variables [$\ln N_E$, ($\ln SIZ_{(n-1)} \cdot \ln YR2$), ($\ln SIZ_{(n-1)} \cdot \ln YR4$), ($\ln DST_{(n-1)} \cdot LO$), and $\ln EL1$] were associated with almost all of this same variation (table 18). In the reduced model, each of these variables is significant beyond $p = 0.005$. The order in which these variables entered the reduced model was:

Step	Variable	R^2
1	$\ln N_E$	0.372
2	($\ln SIZ_{(n-1)} \cdot \ln YR2$)	.516
3	($\ln SIZ_{(n-1)} \cdot \ln YR3$)	.583
4	$\ln EL1$	.606
5	($\ln SIZ_{(n-1)} \cdot \ln YR4$)	.621
5	($\ln SIZ_{(n-1)} \cdot \ln YR3$) replaced by ($\ln DST_{(n-1)} \cdot LO$)	.638

4.3.2.2 IDA(2)—These IDA analyses do not use indices of interstand influences. In model (12), eight variables were associated with the variation in $\ln N_L$, and five of these variables accounted for nearly all of this same variation (table 18). In the reduced model, each variable is significant beyond $p = 0.001$. Here are the variables in order of appearance in the reduced model:

Step	Variable	R^2
1	$\ln N_E$	0.372
2	$\ln YR2$	.491
3	$\ln YR4$	.525
3	$\ln YR2$ replaced by ($\ln N_E \cdot \ln YR3$)	.541
4	$\ln EL1$	.571
5	$\ln EL3$	.585

4.3.2.3 MONT—The MONT analyses used the 428 Montana observations that included estimates of N_E and subsequent N_L. In the model (11), 11 variables were associated with the variation in $\ln N_L$. Among these variables, five accounted for most of this variation (table 19). In the reduced form, each of these variables is significant beyond $p = 0.005$. These variables entered the reduced model as follows:

Step	Variable	R^2
1	$\ln N_E$	0.382
2	$\ln TRT$	.472
3	($\ln WASP \cdot MED$)	.491
4	$\ln SLOPE$	.510
5	($\ln AGE \cdot HI$)	.522

Table 18—Regression coefficients for estimating fourth instars ($\ln N_L$); data from IDA; N = 414

Variable	Model (10) (includes lnSIZ and lnDST) Full	Reduced	Model (12) Full	Reduced
Intercept[a]	1.164	0.935	-0.155	0.875
$\ln SIZ_{(n-1)}$	.650		--	--
$(\ln SIZ_{(n-1)} \cdot \ln YR2)$	3.105	3.284	--	--
$(\ln SIZ_{(n-1)} \cdot \ln YR4)$	-1.840	-1.436	--	--
$(\ln DST_{(n-1)} \cdot LO)$	.984	1.120	--	--
$\ln N_E$	.339	.395	.479	.245
$(\ln N_E \cdot \ln YR3)$	ns[b]		ns	.202
$(\ln N_E \cdot \ln YR4)$	ns		-.286	
$\ln YR3$	ns		.772	
$\ln YR4$	ns		2.408	1.298
$\ln EL1$	-1.022	-.943	-1.483	-1.446
$\ln EL3$	.166		.252	.260
$\ln SASP$	.184		ns	
$\ln DOUG$	ns		.408	
$(\ln TRUE \cdot LO)$	-.452		-.643	
$(\ln AGE \cdot LO)$	.471		ns	
$(\ln VCD \cdot MED)$	-.665		ns	
R^2	.666	.638	.609	.585
RTMSE	.633	.653	.681	.699

[a] Intercept corrected for logarithmic bias.
[b] Not significant.

Table 19—Regression coefficients for estimating fourth instars ($\ln N_L$) using model (11); data from MONT; N = 428

Variable	Full model	Reduced model
Intercept[a]	-1.207	0.015
$\ln N_E$	.345	.390
$\ln TRT$	-.313	-.405
$\ln ELEV$	.609	
$\ln SLOPE$	.501	.575
$(\ln WASP \cdot MED)$	-.963	-1.090
$(\ln WET \cdot MED)$	.305	
$\ln PROD$	.138	
$(\ln DOUG \cdot MED)$	-.857	
$(\ln AGE \cdot LO)$	-1.315	
$(\ln AGE \cdot HI)$	.595	.577
$\ln VCD$	-.443	
R^2	.557	.522
RTMSE	.601	.620

[a] Intercept corrected for logarithmic bias.

4.3.2.4 NMEX—For the NMEX analyses, I used the 324 observations from the New Mexico Suppression Project that included estimates of N_E and subsequent N_L. In the model (12), 10 variables accounted for most of the variation in lnN_L, and five of them accounted for almost all of this same variation (table 20). In the reduced model, each of these variables is significant beyond $p = 0.001$. The variables entered the model in the following order:

Step	Variable	R^2
1	lnTRT	0.471
2	lnN_E	.611
3	lnEL5	.638
4	lnSTK	.654
5	$(lnN_E \cdot lnYR3)$	.666
5	lnSTK replaced by (lnSTK $\cdot$ MED)	.669

4.3.2.5 DAMAG—Data accumulated to evaluate damage caused by the budworm in DAMAG provide a particularly precise set of estimates of N_M, N_L, and DEF. For this analysis, I used the 63 observations that included estimates of N_E and subsequent N_L. When model (13) was tested against these data, two variables were significantly related to variation in lnN_L. Together, these variables accounted for about 67 percent of the variation in lnN_L. Here are the variables, in the order they entered the model:

Step	Variable	R^2
1	lnN_E	0.504
2	lnYR2	.670

The following equation (37) describes the relation between N_L and these variables:

Year is similar to 1978-79:
$$N_L = 3.10 \cdot N_E^{.381} . \tag{37A}$$

Year is similar to 1979-80, 1980-81, or 1981-82:
$$N_L = 1.39 \cdot N_E^{.381} . \tag{37B}$$

4.3.2.6 COLO, PNW, and SAMP—Several environmental attributes possibly related to budworm population dynamics are either poorly represented or missing among the 59 observations in the combined data set from COLO, PNW, and SAMP. Despite this shortcoming, this small data set provided an opportunity to evaluate some suspected environmental determinants of N_L in plots drawn from an extremely large geographic area (Oregon, Washington, Idaho, Montana, and Colorado). Consequently, values of lnN_L derived from the plots in these three studies were regressed against lnN_E and the logarithms of all available indices of site and stand conditions, by using model (14). In this model, six variables were significantly related to the variation in lnN_L, and accounted

for about 90 percent of this variation ($R^2 = 0.895$). Here are the variables, in their order of appearance:

Step	Variable	R^2
1	PNW	0.410
2	($\ln N_E \cdot$ PNW)	.814
3	($\ln$VCD $\cdot$ PNW)	.838
4	($\ln$DOUG $\cdot$ PNW)	.861
5	($\ln$WET $\cdot$ SAMP)	.882
6	($\ln$AGE $\cdot$ PNW)	.895

Equation (38) describes the relation between N_L and these variables:

Situation similar to that in COLO:
$$N_L = 55.08 . \tag{38A}$$

Situation similar to that in PNW:
$$N_L = 0.079 \, N_E^{1.068} \cdot \text{DOUG}^{-1.681} \cdot \text{AGE}^{3.092} \cdot \text{VCD}^{-1.966} . \tag{38B}$$

Situation similar to that in SAMP:
$$N_L \text{ in wet sites} = 97.79; \text{ else } N_L = 55.08 . \tag{38C}$$

Table 20—Regression coefficients for estimating fourth instars ($\ln N_L$) using model (12); data from NMEX; N = 324

Variable	Full model	Reduced model
Intercept[a]	0.512	0.582
$\ln N_E$	.335	.360
($\ln N_E \cdot \ln$YR3)	.248	.080
$\ln$YR3	-.976	
$\ln$TRT	-1.436	-1.612
($\ln$TRT $\cdot$ MED)	-.515	
$\ln$EL1	.418	
$\ln$EL2	.223	
$\ln$EL5	-1.432	-1.592
($\ln$SLOPE $\cdot$ LO)	.685	
($\ln$STK $\cdot$ MED)	.402	.441
R^2	.700	.669
RTMSE	.768	.800

[a] Intercept corrected for logarithmic bias.

4.3.2.7 OREG—The 47 observations that include estimates of both N_E and subsequent N_L from the most recent outbreak in eastern Oregon (OREG) provide an opportunity to test not only for relations among successive densities, but also to examine the parameters relating these densities to possible systematic year-to-year changes. Consequently, values of $\ln S_S$ derived from the plots in OREG were regressed against $\ln N_E$ and the logarithm of a year index ($\ln$YRIDX) by using model (15). In this model, both of the independent variables were significant beyond $p = 0.005$, and accounted for about 62 percent of the variation in $\ln S_S$ ($R^2 = 0.623$). Here is their order of appearance in the model:

Step	Variable	R^2
1	$\ln N_E$	0.535
2	$\ln YRIDX$	.623

The equation that relates these variables to N_L is as follows:

Year similar to 1981-85:
$$N_L = 27 N_E^{.161}.\tag{39A}$$

Year similar to 1986-88:
$$N_L = 10.3 N_E^{.161}.\tag{39B}$$

4.3.2.8 WXBASE—In the WXBASE data, 245 observations included estimates of both $N_{E(n)}$ and $N_{E(n+1)}$ and the eight weather indices specified in model (16). Together, the nine independent variables were associated with about 50 percent of the variation in $\ln N_{E(n+1)}$ ($R^2 = 0.499$). Here are the variables, in their order of appearance:

Step	Variable	R^2
1	$\ln N_{E(n)}$	0.386
2	$\ln SUMT$	.403
3	$\ln MAY1$	.419
4	$\ln MAY3$	.441
5	$\ln PCP2$	.453
6	$\ln PCP1$	.465
7	$\ln MAY2$	.481
8	$\ln MART$	.490
9	$\ln JANT$	.499

Equation (40) relates these variables to $N_{E(n+1)}$:
$$N_{E(n+1)} = 52.15 \cdot N_{E(n)}^{.576} \cdot JANT^{-.886} \cdot MART^{-1.296} \cdot MAY1^{-2.768} \cdot MAY2^{-1.857}$$
$$\cdot MAY3^{-1.060} \cdot PCP1^{-1.125} \cdot SUMT^{-1.368} \cdot PCP2^{.754}.\tag{40}$$

4.3.3 Relations Specified by the Results

4.3.3.1 Density dependence—Relations between N_E and subsequent S_s are displayed for the prolonged outbreaks in Idaho, Montana, and New Mexico (figs. 6-8); for the outbreak in DAMAG (fig. 9); for the nonoutbreak PNW populations (fig. 10); and for the outbreak in OREG (fig. 11). All the prolonged outbreaks (fig. 6-8) were clearly subjected to severe density-dependent mortality. Across this same density range, S_s was virtually constant in the suboutbreak PNW populations (fig. 10).

To my knowledge, the drastic decline in S_s across a broad range in density was first reported for outbreak western budworm populations in Campbell (1987). At that time, I speculated that this relation might reflect some sort of intraspecific competition—either for hibernation sites or for food. My view has since been modified and is expanded considerably in sections 5.2.3 and 5.2.5.
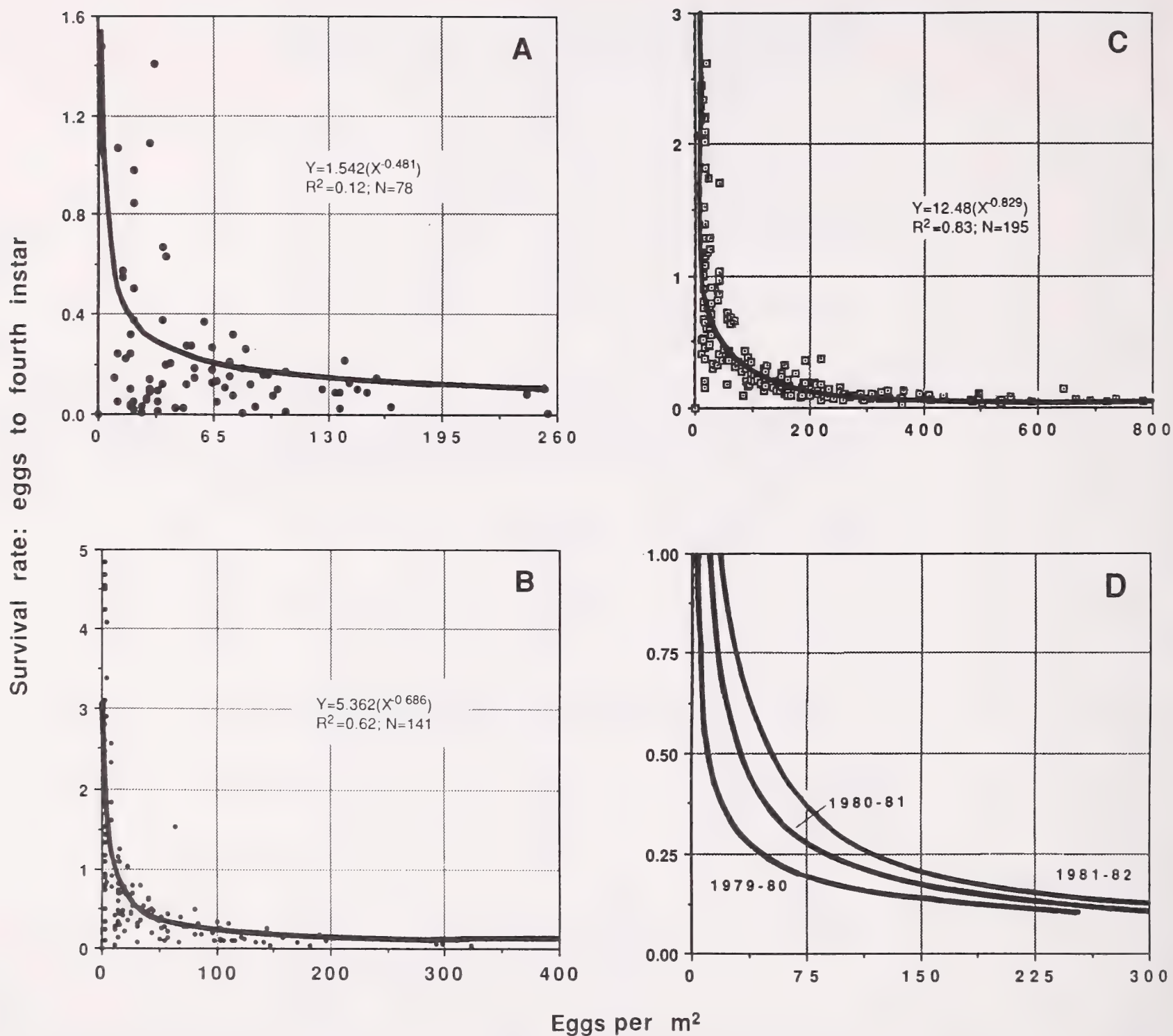
Figure 6—Egg density and survival rate from eggs to fourth instar in IDA: A, 1979-80; B, 1980-81; C, 1981-82; D, comparison, 1979-80, 1980-81, and 1981-82.

4.3.3.2 Parameter stability across budworm density—Earlier (section 4.2.2.2), I noted that relations between environmental attributes and the number of eggs per mass (EG) were sometimes unstable across a broad range in budworm density. This same caveat applies as the insects pass from eggs to half-grown larvae. For example, the relations derived for MONT (table 19) show that budworm survival was inversely related to stand age in plots where N_E did not exceed 100 eggs per m². But, in plots where N_E was high ($N_E > 500$), budworm survival was higher in the older stands.
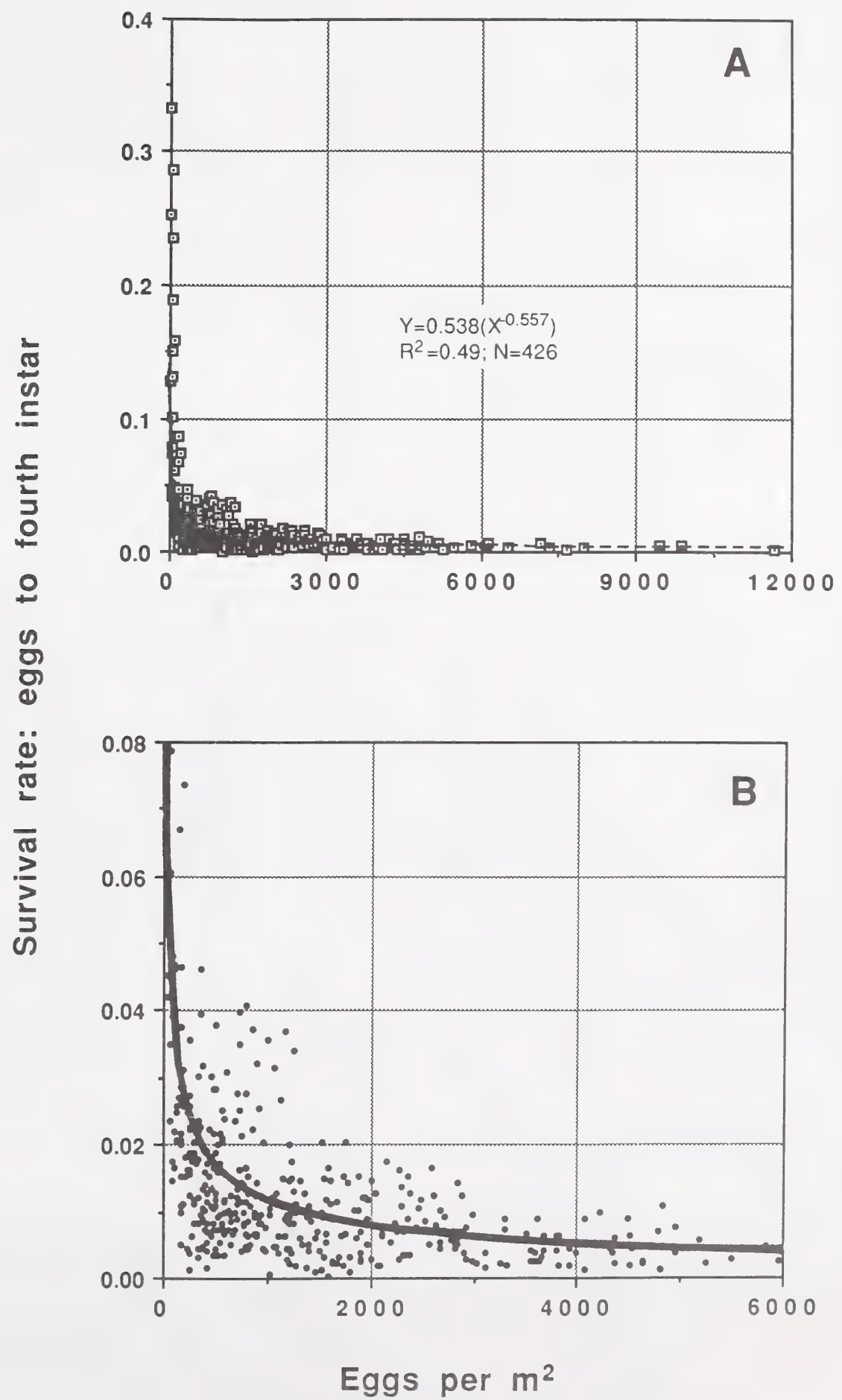
Figure 7—Egg density and survival rate from eggs to fourth instar in MONT: A, all observations; B, detail showing principal change in relation between density and survival.
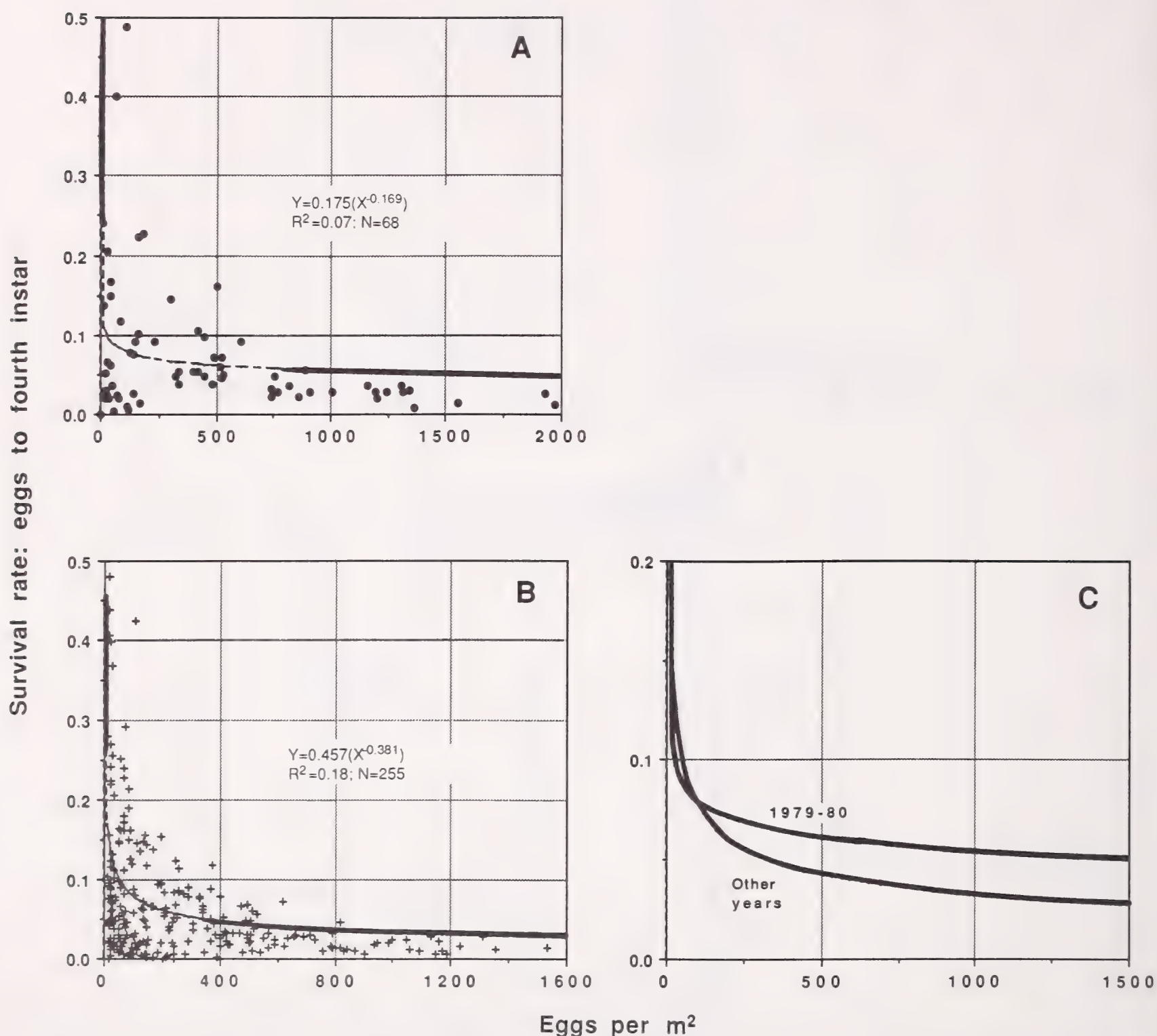
Figure 8—Egg density and survival rate from eggs to fourth instar in NMEX: A, 1979-80; B, 1977-78 and 1978-79; C, comparison, 1979-80 and other years.

4.3.3.3 Differences across years—For any given value of N_E, average S_S in IDA was highest in 1981-82, intermediate in 1980-81, and lowest in 1979-80 (fig. 6). In DAMAG, S_S was significantly higher during the first season (1978-79) than in the subsequent years of the project (fig. 9). In NMEX, average S_S was also significantly higher in 1979-80 than in either 1977-78 or 1978-79 (fig. 8). And in OREG, S_S was higher during 1981-85 than during 1985-88 (fig. 11). Processes that may be responsible for these year-to-year differences are discussed in section 5.2.3.
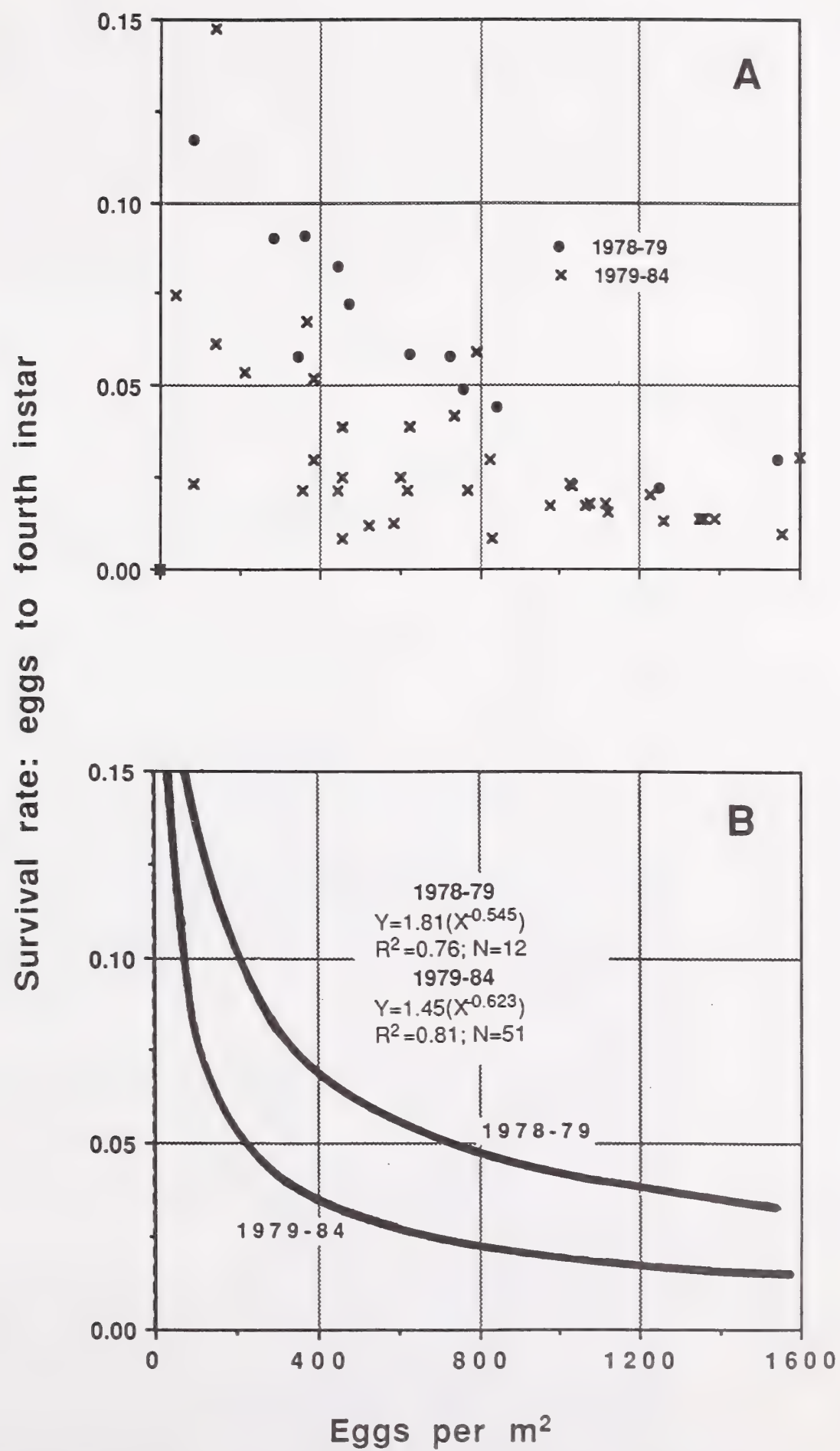
Figure 9—Egg density and survival rate from eggs to fourth instar in DAMAG: A, scatter diagram, 1978-79 and other years; B, comparison, 1978-79 and other years.
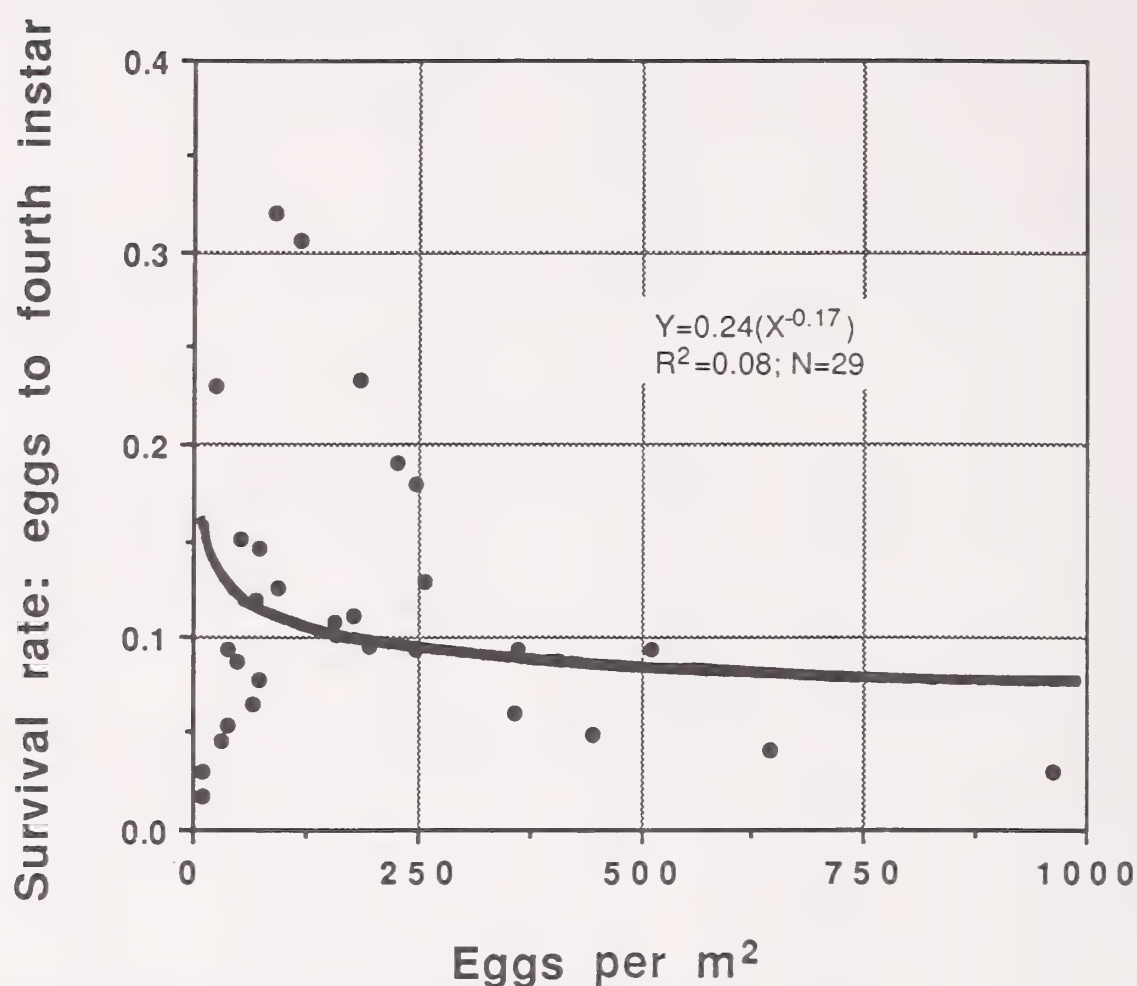
Figure 10—Egg density and survival rate from eggs to fourth instar in PNW.

4.3.3.4 Influence of recent insecticide treatment—Average S_s was lower in treated than untreated plots during posttreatment years in both MONT (fig. 12) and NMEX (fig. 13). In each area, the plots were examined for systematic differences as a function of years since insecticide treatment. Contrary to my expectation, these results do not suggest that the difference in S_s between treated and untreated plots declined from one year to the next.

The above results are just the opposite of those reported by MacDonald (1963a) for eastern budworm populations in New Brunswick that had been treated with DDT. MacDonald reported survival rates of 0.402, 0.305, and 0.372 for treated populations in their first, second, and third posttreatment years, respectively, compared to an average S_s of 0.196 in unsprayed check plots. A rationale that might account for these conflicting results is described in section 5.2.5.

4.3.3.5 Interstand influences—In IDA, most of the variation in lnN_L was associated with lnN_E, and interactions between year and an index of outbreak size (SIZ). The relation between S_s and SIZ differed from year to year. In 1979-80, SIZ and S_s increased together; in 1980-81, they continued to increase together but at a much lower rate. In 1981-82, S_s decreased as SIZ increased. Underlying processes that may have caused the shifting relation between outbreak size and S_s in IDA are considered in section 5.2.3.

At low densities, S_s in IDA was inversely related to the distance from a plot to the edge of visible defoliation (fig. 14). This correlation undoubtedly resulted, in part, from movements of the tiny larvae during fall and spring dispersal.
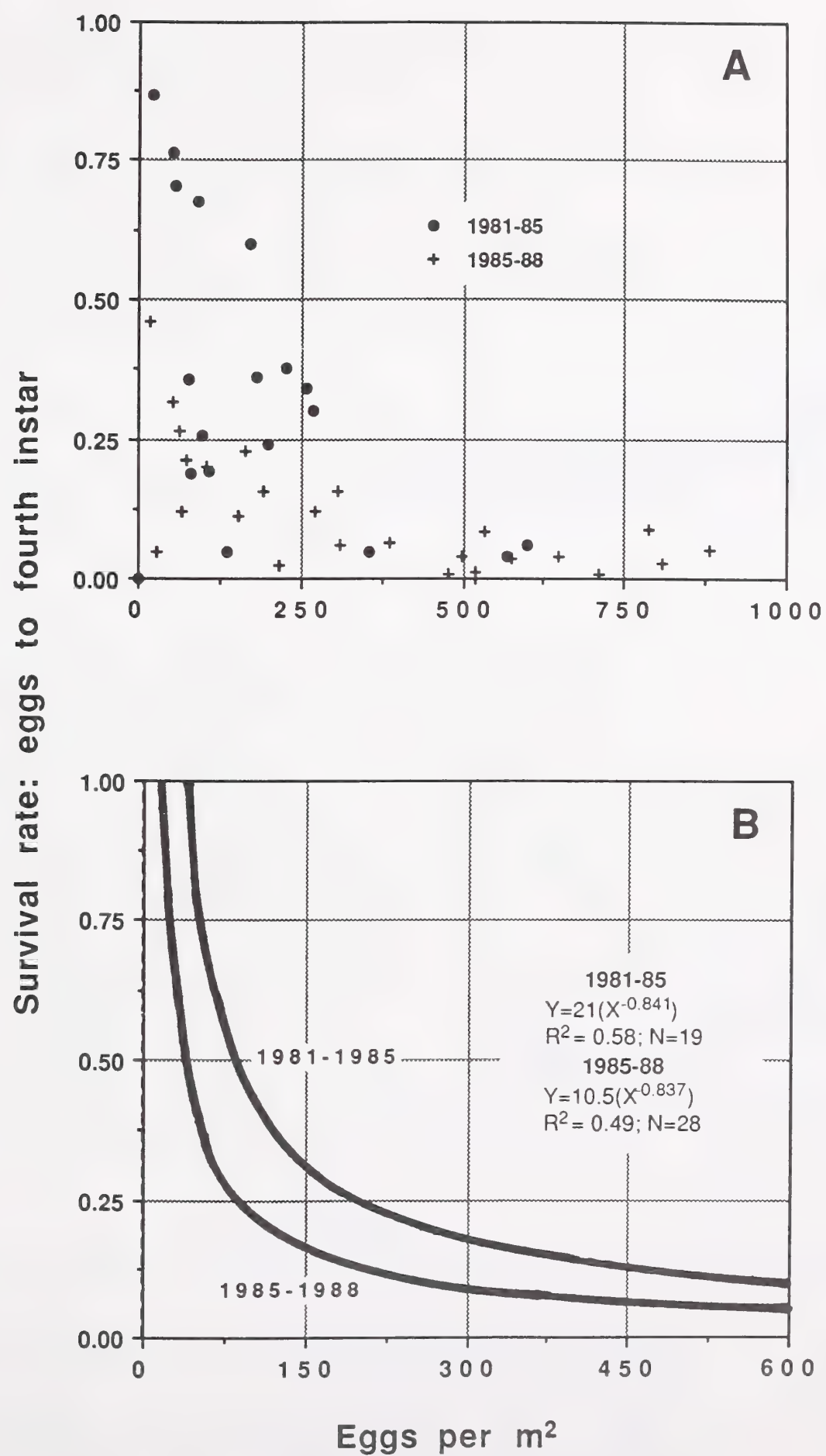
Figure 11—Egg density and survival rate from eggs to fourth instar in OREG: A, scatter diagram, 1981-85 and 1985-88; B, comparison, 1981-85 and 1985-88.
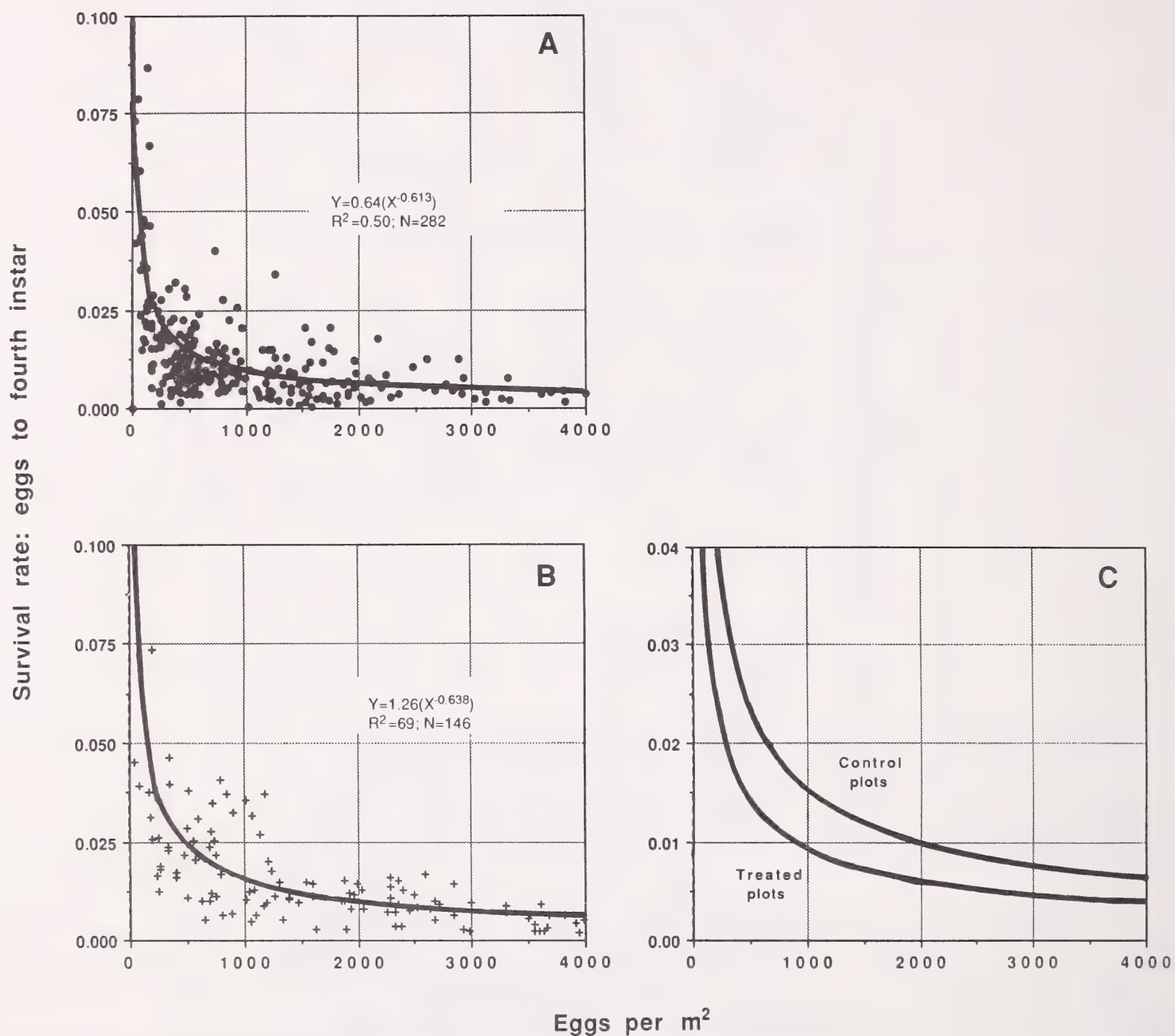
Figure 12—Egg density and survival rate from eggs to fourth instar after insecticide treatment in MONT: A, treated plots; B, control plots; C, comparison, treated and control plots.

4.3.3.6 Influence of site—The indices of site conditions most consistently related to S_s were elevation, slope, and aspect.

Elevations were estimated for the plots in IDA, MONT, NMEX, and DAMAG, and S_s was related to indices of elevation in three of the four areas. In NMEX, for example, mean values of S_s in both the highest elevation stratum (EL5) and in other strata were:
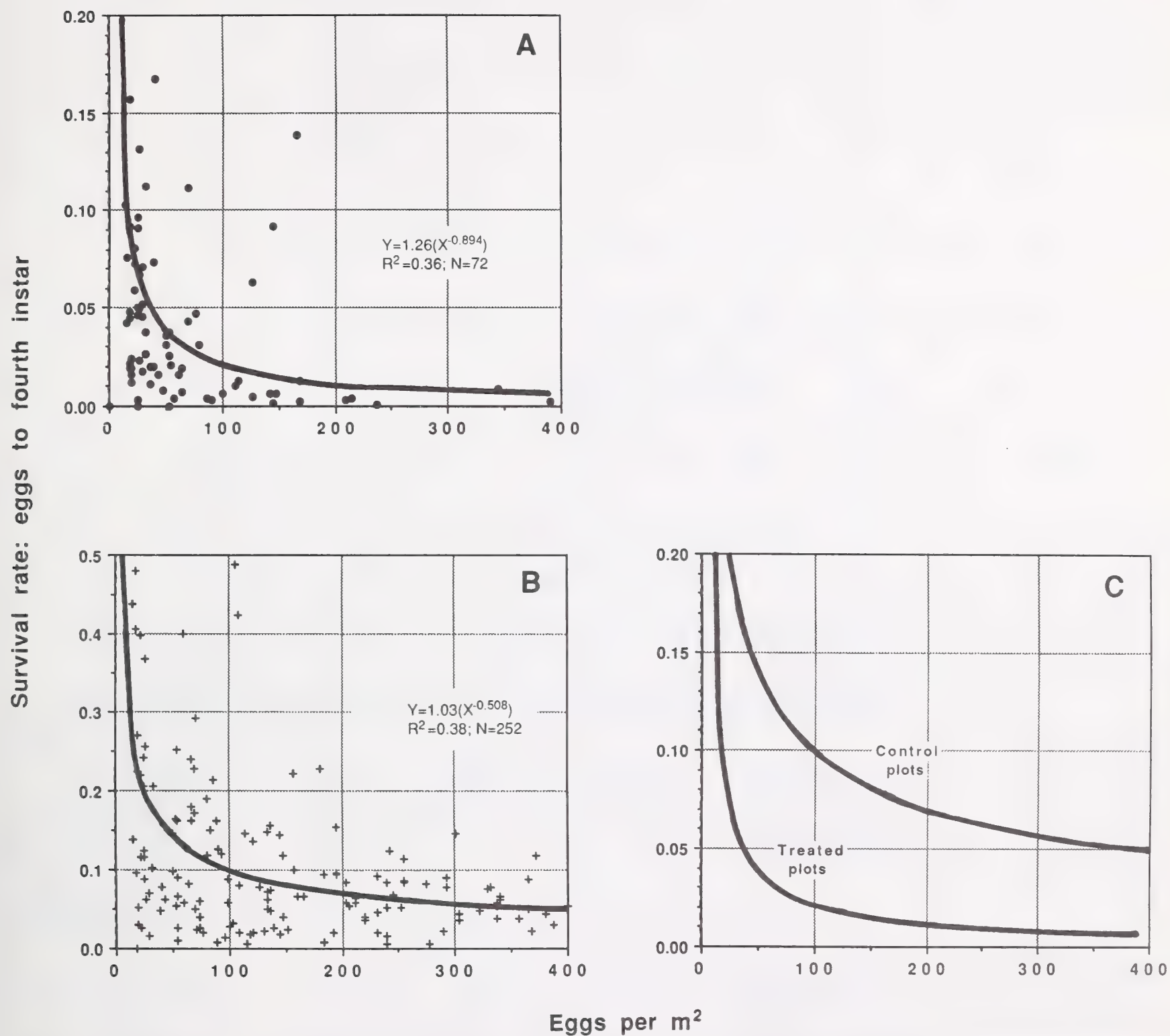
Figure 13—Egg density and survival rate from eggs to fourth instar after insecticide treatment in NMEX: A, treated plots; B, control plots; C, comparison, treated and control plots.

Y-axis: Survival rate: eggs to fourth instar

X-axis: Eggs per m^2

Plot A: $Y=1.26(X^{-0.894})$; $R^2=0.36$; $N=72$

Plot B: $Y=1.03(X^{-0.508})$; $R^2=0.38$; $N=252$

Plot C: Control plots; Treated plots

Plot category	Number of plot-years	Mean S_s	Standard error
EL5	10	0.021	0.009
Other	349	.067	.005
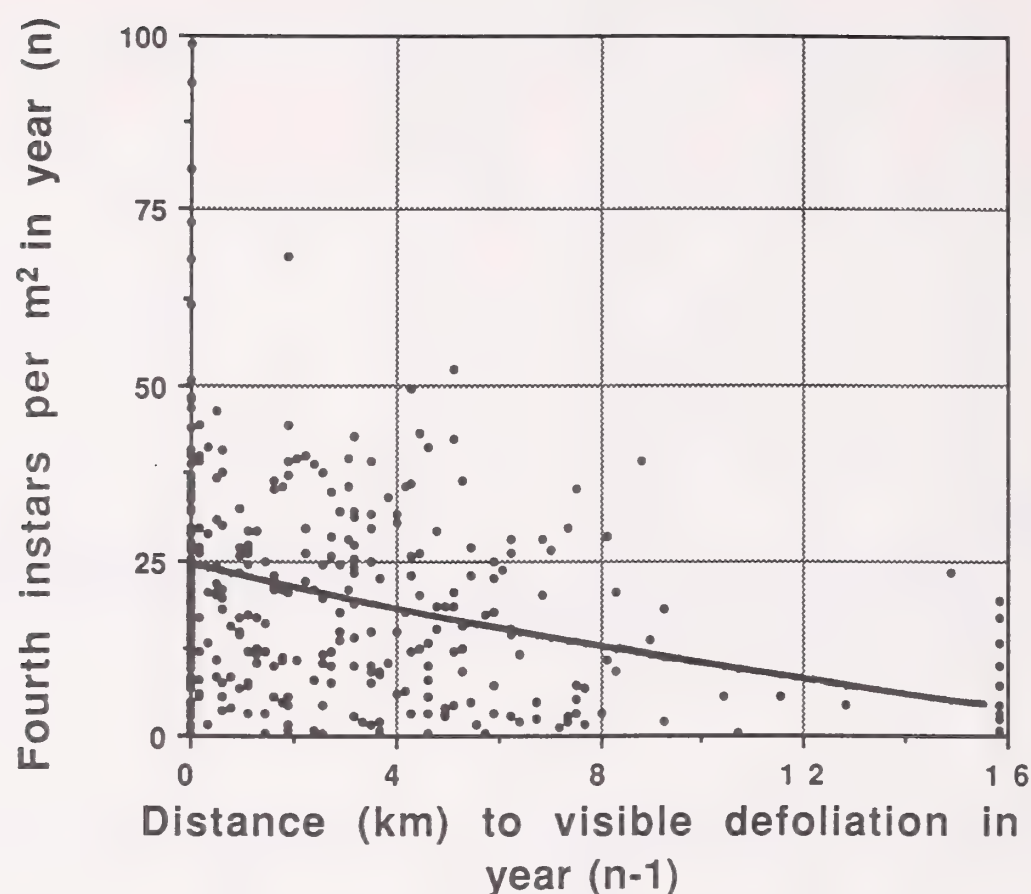
Figure 14—Distance to visible defoliation in year (n-1) and fourth-instar density in year (n) in IDA; $N_E \leq 100$ eggs per m².

In two of the largest data sets (IDA and MONT), S_s was related to aspect. Here, for example, are mean values of S_s in MONT on both west-facing slopes and other aspects:

Plot category	Number of plot-years	Mean S_s	Standard error
West-facing	6	0.0054	0.0013
Other aspects	103	.0201	.0014

In two data sets (MONT and NMEX), S_s was related to slope. Again in MONT, here are mean values of S_s on slopes in various categories:

Plot category	Number of plot-years	Mean S_s	Standard error
≤ 10% slope	178	0.012	0.001
11-25% slope	182	.021	.003
26-40% slope	52	.024	.006
≥ 40% slope	16	.020	.006

I have no doubt that associations between S_s and elevation, slope, and aspect reflect an underlying cause and effect relation between temperature and budworm survival. As noted by Shepherd (1985) for western budworm populations in British Columbia, "The time of larval emergence and dispersal relative to bud development is critical."

4.3.3.7 Influence of stand—In PNW, IDA (at low egg densities), and MONT (at high ones), S_s and stand age increased together. In MONT, here are mean values of S_s as

they were related to stand age during plot-years when egg density was high:

Plot category	Number of plot-years	Mean S_s	Standard error
$\leq$ 50 yr old	95	0.007	0.0005
51-75 yr	109	.009	.0006
76-150 yr	69	.013	.0013
> 150 yr	21	.013	.0019

A process that might account for the direct relation between S_s and stand age is suggested in section 5.2.3.1.

In NMEX, S_s was higher in fully stocked stands. Mean values of S_s in NMEX are shown below for plots where stocking was either below average or at least average for the area:

Plot category	Number of plot-years	Mean S_s	Standard error
Understocked	169	0.061	0.006
Average to above	155	.086	.009

Mott (1963a) showed that S_s in the eastern budworm was inversely related to tree diameter. He attributed this relation to an inverse relation between tree diameter and stocking in that particular part of New Brunswick, and cautioned that his results pertained only to the outbreak conditions when the data were collected. Subsequently, however, Kemp and Simmons (1979) derived results similar to those of Mott from a study conducted in north-central and eastern Maine. I believe the positive relation between S_s and stocking (in NMEX) arises in large part from the same dispersal processes noted by Mott as probable causes for this phenomenon in the eastern budworm.

Increased densities of foliage-foraging ants in the open stands associated with drier sites also may be contributing to low values of S_s. Specifically, Youngs (1985) found higher densities of each common predaceous ant species "...across almost all [western budworm] habitat types...." in stands where average canopy coverage was less than 90 percent. Similarly, Jennings (1971) identified six species of ants that preyed on the jack pine budworm on xeric sites in Wisconsin.

4.3.3.8 Influence of weather—Coupled with recent papers on relations between weather and the western budworm (Hard and others 1980, Kemp and others 1985), the systematic year-to-year differences found in budworm survival in all of the major data bases provided a powerful incentive to examine WXBASE for possible links between weather and changes in budworm numbers. Links implicated by that analysis are summarized below.

When mean January temperature dropped below about -13 °C, subsequent egg-mass production was reduced by about 59 percent (equation 40). Conversely, budworm survival varied inversely with temperature during March.

Survival dropped drastically (by about 94 percent) when mean May temperature dropped below about 5.7 °C, and continued to be reduced significantly until mean May temperature rose above about 8.8 °C (fig. 15). Survival was also reduced by about 75 percent in 52 of 250 plot-years in which mean June temperature was less than about 0.8 °C warmer
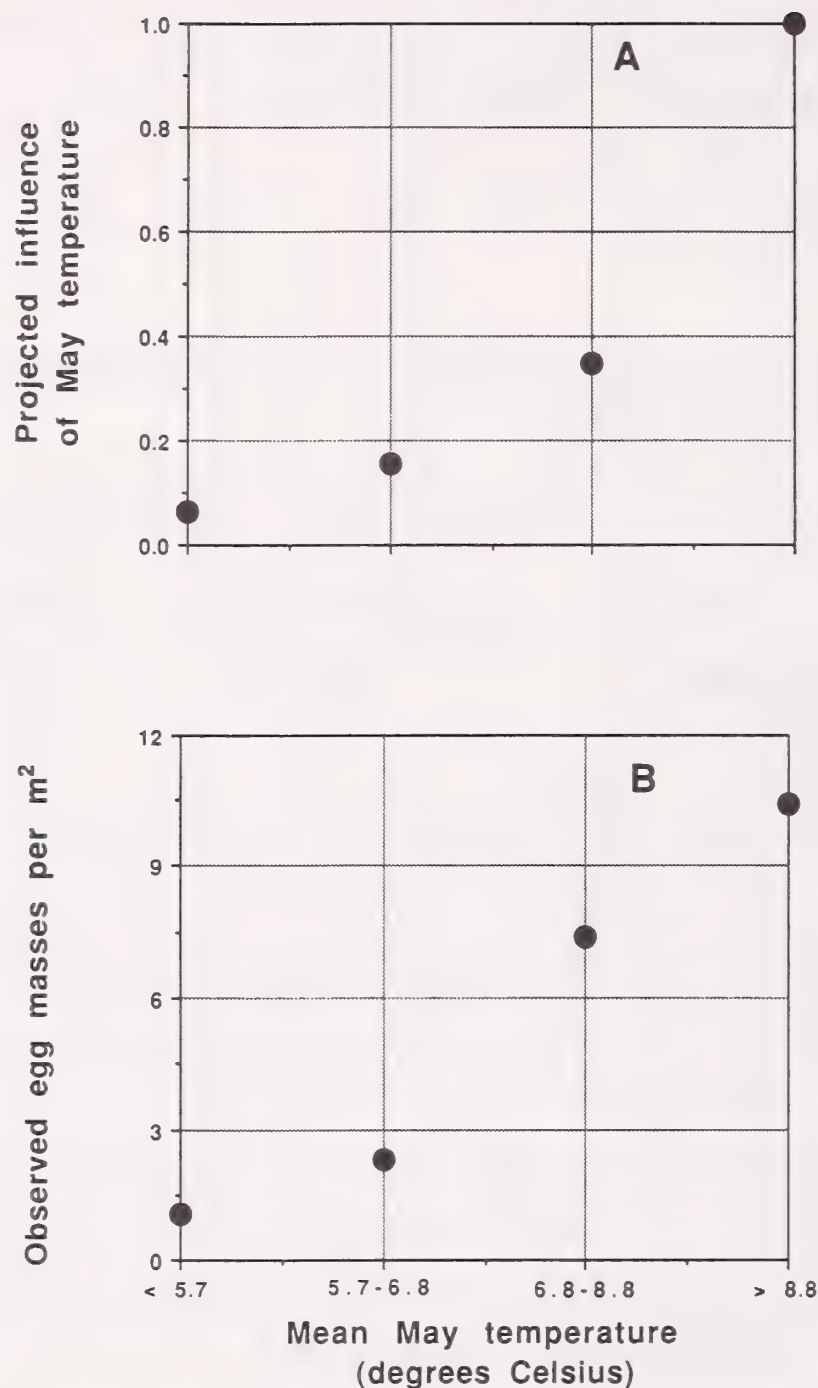
Figure 15—Influence of mean May temperature on density in WXBASE; A, influence projected by the coefficients in equation (40); B, mean egg-mass densities at the end of the generation.

than had been recorded for May of the same year.

Budworm survival varied inversely with the average amount of precipitation during rainy days in May, and it was about 53 percent higher when precipitation during May and June was less than 8.4 cm.

Some processes that are suggested by the above results are discussed in section 5.2.6.

**4.4
Projecting Defoliation**

Preliminary examination of the IDA and WXBASE data suggested that interstand influences were not related to defoliation during the interval from fourth instar to pupation. Consequently, indices of interstand influences (SIZ and DST) will not be evaluated further as possible determinants of DEF.

4.4.1
The Equations

4.4.1.1 IDA—To evaluate model (19), I used the 299 IDA plot-years that include nonzero estimates of both N_L and subsequent DEF. These data were drawn during 1980 (year 2) and 1981 (year 3). Eleven variables were associated with variation in lnDEF, and five of these variables accounted for most of this variation (table 21). In the reduced model, each of these variables is significant beyond $p = 0.005$. These variables entered the model as follows:

Step	Variable	R^2
1	$(\ln N_L \cdot \ln YR3)$	0.531
2	$(\ln N_L \cdot \ln YR2)$	.573
3	lnTRT	.589
4	$(\ln TRUE \cdot HI)$	.604
5	lnHISH	.616

4.4.1.2 MONT—For the MONT analyses, I used the 428 plot-years that included estimates of N_L and DEF in 1982 (year 2) and 1983 (year 3). Among the nine variables in model (18) that were associated with variation in lnDEF, three accounted for most of this variation (table 22). In the reduced form, each of the three variables is significant beyond $p = 0.001$. These variables entered the reduced model as follows:

Step	Variable	R^2
1	$\ln N_L$	0.590
2	lnYR2	.716
3	lnTRT	.769

4.4.1.3 NMEX—To evaluate model (19) in NMEX, I used the 432 plot-years that include both nonzero estimates of N_L and estimates of subsequent DEF. These data were drawn during 1978 (year 2), 1979 (year 3), and 1980 (year 4). Here, 12 variables were associated with about 78 percent of the variation in lnDEF. In the reduced model, 4 of these 12 variables, each significant beyond $p = 0.001$, accounted for almost as much of this same variation (table 23). Here are these four variables, in their order of appearance:

Step	Variable	R^2
1	$\ln N_L$	0.657
2	lnYR4	.707
3	$(\ln SPR \cdot HI)$	.728
4	lnTRT	.741

4.4.1.4 DAMAG—For this analysis, I used the 67 plot-years from DAMAG that include estimates of both N_L and DEF. When these data were tested against model (20), three variables were statistically significant. Here are the variables, in their order of appearance:

Step	Variable	R^2
1	$\ln N_L$	0.776
2	lnYR4	.836
3	lnWASP	.846

Table 21—Regression coefficients for estimating defoliation (lnDEF) using model (19); data from IDA; N = 299

Variable	Full model	Reduced model
Intercept[a]	-0.250	-0.037
$(lnN_L \cdot lnYR2)$	.080	.060
$(lnN_L \cdot lnYR3)$	.229	.198
lnTRT	-.069	-.083
lnSASP	-.087	
$(lnWET \cdot HI)$	.177	
$(lnDOUG \cdot LO)$	.335	
$(lnDOUG \cdot HI)$	.513	
$(lnTRUE \cdot HI)$	.516	.353
$(lnSPR \cdot MED)$	.322	
$(lnVCD \cdot HI)$	.337	
lnHISH	-.069	-.070
R^2	.667	.616
RTMSE	.182	.193

[a] Intercept corrected for logarithmic bias.

Table 22—Regression coefficients for estimating defoliation (lnDEF) using model (18); data from MONT; N = 428

Variable	Full model	Reduced model
Intercept[a]	-0.482	-0.050
lnN_L	.110	.149
$(lnN_L \cdot lnYR2)$	.080	
lnYR2	-.394	-.226
lnTRT	-.142	-.149
$(lnTRT \cdot HI)$	.082	
lnELEV	.150	
lnWASP	-.075	
lnDOUG	.381	
$(lnHISH \cdot LO)$	.074	
R^2	.798	.769
RTMSE	.121	.128

[a] Intercept corrected for logarithmic bias.

The following equation (41) was derived from this analysis:

Year is similar to 1981:
$$DEF = 0.706 \cdot N_L^{.216} \cdot WASP^{.072}. \tag{41A}$$

Year is similar to 1979, 1980, or 1982:
$$DEF = 0.56 \cdot N_L^{.216} \cdot WASP^{.072}. \tag{41B}$$

Table 23—Regression coefficients for estimating defoliation (lnDEF) using model (19); data from NMEX; N = 432

Variable	Full model	Reduced model
Intercept[a]	-0.666	-0.525
lnN_L	.068	.112
$(lnN_L \cdot lnYR4)$	.029	
lnYR4	.109	.138
lnTRT	-.275	-.102
$(lnTRT \cdot LO)$	.220	
lnEL1	-.035	
$(lnPROD \cdot MED)$	.070	
$(lnSPR \cdot LO)$	-.172	
$(lnSPR \cdot MED)$	-.408	
$(lnSPR \cdot HI)$	-.650	-.248
$(lnAGE \cdot MED)$	-.275	
$(lnHISH \cdot HI)$	-.213	
R^2	.780	.741
RTMSE	.146	.157

[a] Intercept corrected for logarithmic bias.

4.4.1.5 WXBASE—For this analysis, I used the 248 plot-years in WXBASE that include estimates of both $N_{M(n-1)}$ and defoliation in years (n-1) and (n). When regression model (21) was tested against these data, both $N_{M(n-1)}$ and $DEF_{(n-1)}$ were associated with $DEF_{(n)}$ beyond p = 0.001. Here is the order in which these variables entered the model:

Step	Variable	R^2
1	$lnN_{M(n-1)}$	0.419
2	$lnDEF_{(n-1)}$	.451

The following equation (42) describes how these variables are related to DEF:

$$DEF_{(n)} = 1.604 \cdot N_{M(n-1)}{}^{.275} \cdot DEF_{(n-1)}{}^{.246}. \tag{42}$$

**4.4.2
Defoliation of
Douglas-Fir Versus
White Fir**

After excluding treated plots in the year of treatment (1977), percentage of defoliation on white fir in the remaining 180 NMEX plot-years was examined as a function of percentage of defoliation on the adjacent Douglas-fir. From model (22), the following equation (43) was derived:

$$Defol_{(white)} = 100 - .00985[100-Defol_{(Doug)}]^2. \tag{43}$$

For the NMEX plot-years, this zero-based equation accounted for about 95 percent of the total variation in percentage of defoliation on white fir (R^2 = 0.954).

**4.4.3
Relations Specified
by the Results**

4.4.3.1 Density dependence—As expected, defoliation increased with increasing fourth-instar density (figs. 16-19). Even at very low densities, defoliation usually approached 20 percent in the outbreak conditions described by these data. In DAMAG, an area that was being subjected to a new outbreak, average projected defoliation of current-year foliage approached 100 percent as N_L exceeded 50 larvae per m^2 (fig. 19). In both IDA and NMEX, average projected defoliation usually remained below 100 percent, even at very high densities (fig. 20). These results support the conclusion of Bullard and Young (1980) that "substantial variability exists [among areas] in the relationship between...density and...defoliation...."

4.4.3.2 Parameter stability across budworm density—As was found in preceding sections (see 4.2.2.2 and 4.3.3.2), relations between lnDEF and environmental attributes were sometimes unstable across a broad range in density. For example, the relations shown in table 23 suggest that the proportion of spruce in the overstory foliage had a greater depressing effect on defoliation in NMEX when egg-mass density was high than at lower densities. Implications arising from these unstable relations are discussed in sections 5.2.7 and 5.3.1.3.

4.4.3.3 Differences across years—All areas exhibited significant year-to-year differences in the relation between density and defoliation (figs. 16-19).

In their 1980 paper, Bullard and Young project much higher defoliation per budworm during the first year of an outbreak, with a gradual decline thereafter. Undoubtedly, the declining value of S_S as an outbreak progresses (section 4.3.3.3) was one principal cause of the association these authors found between $N_{M(n-1)}$ and subsequent defoliation. In addition, the higher defoliation trajectories in the new outbreak in DAMAG also support Bullard and Young's (1980) suggestion that defoliation is related to the age of the infestation per se.

4.4.3.4 Influence of recent insecticide treatment—In all three of the areas treated with an insecticide, average defoliation during posttreatment years was lower in the treated blocks (figs. 21C, 22C, and 23C). Further, mean percentage of defoliation in both treated and control blocks in NMEX, which is summarized in figure 24 for 1977 through 1983, continued to be lower in the treated blocks for six posttreatment years. Processes that might account for these associations are discussed in section 5.2.3 and 5.2.5.

4.4.3.5 Influence of prior defoliation—In WXBASE, the defoliation projected from any given N_L was directly related to the amount of defoliation during the preceding year (equation 42). This relation supports prior observations on phenotypic variation in defoliation among host trees (Cates and others 1983, McDonald 1981, Redak and Cates 1984).

4.4.3.6 Influence of site—Two of the four areas (MONT and NMEX) showed slight but statistically significant relations between elevation and defoliation. In NMEX, defoliation was lower among the plots in the lowest portion of the elevational range. In MONT, defoliation and elevation increased together across the observed elevational range. Other investigators have found that defoliation was greatest across an elevational midrange, and less at both minimum and maximum elevations (Heller and Kessler 1985, Marsden and others 1986, Shepherd 1985).
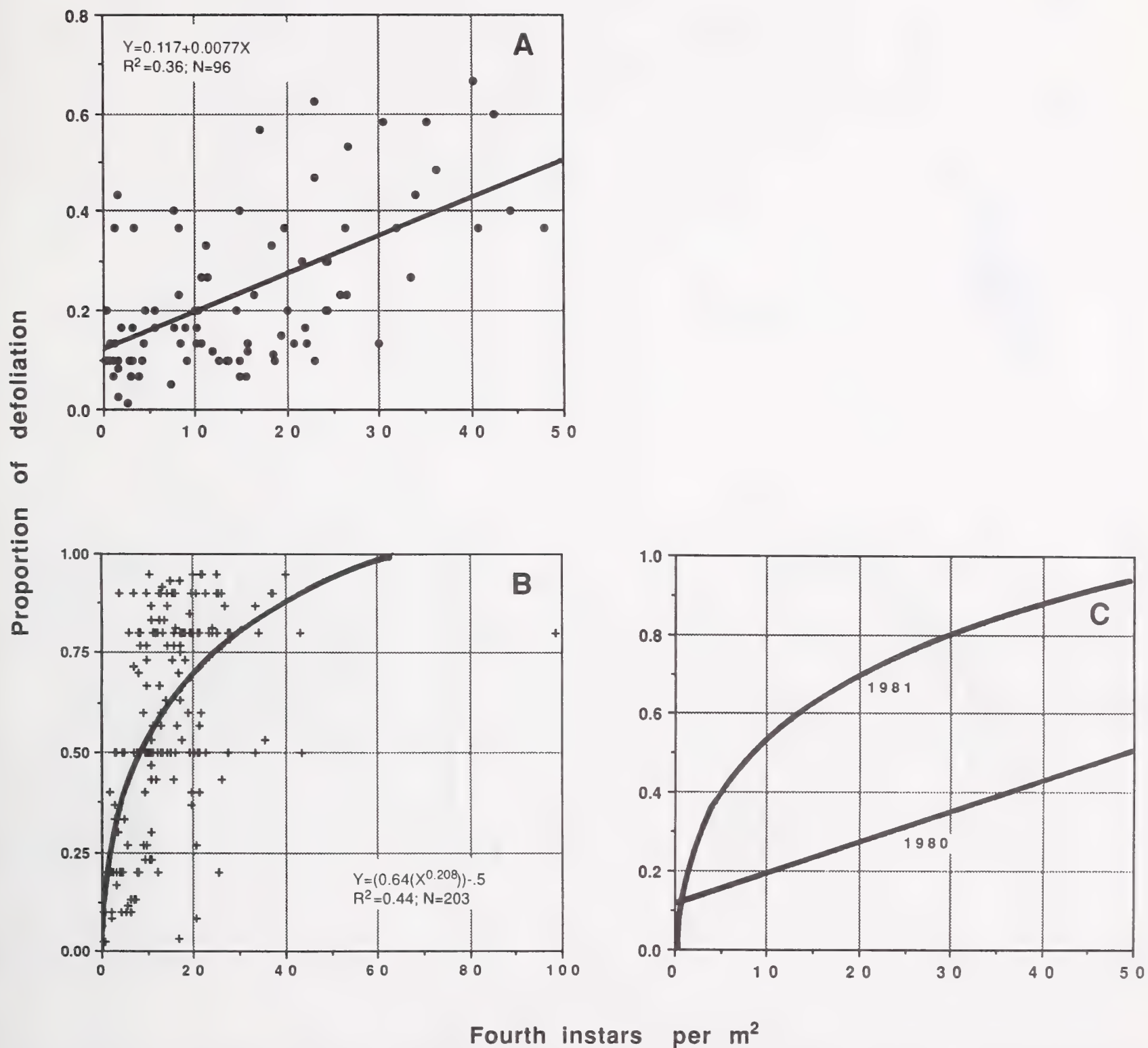
Figure 16—Fourth-instar density and subsequent defoliation in IDA: A, 1980; B, 1981; C, comparison, 1980 and 1981.

As previously noted (section 4.3.3.6), budworm survival from eggs to half-grown larvae (S_s) is a function of elevation. Thus, the association found by other investigators between elevation and defoliation undoubtedly reflects an underlying association between temperature and S_s. In addition, these data also suggest that budworm survival from fourth instar to pupae may be particularly low in the lower portion of the elevational range of budworm host stands.

Proportion of defoliation (y-axis)

Panel A:
$$Y=(0.60(X^{0.229}))-0.5$$
$$R^2=0.60;\ N=214$$

Panel B:
$$Y=(0.85(X^{0.155}))-0.5$$
$$R^2=0.55;\ N=214$$

Panel C: 1983, 1982

Fourth instars per m² (x-axis)
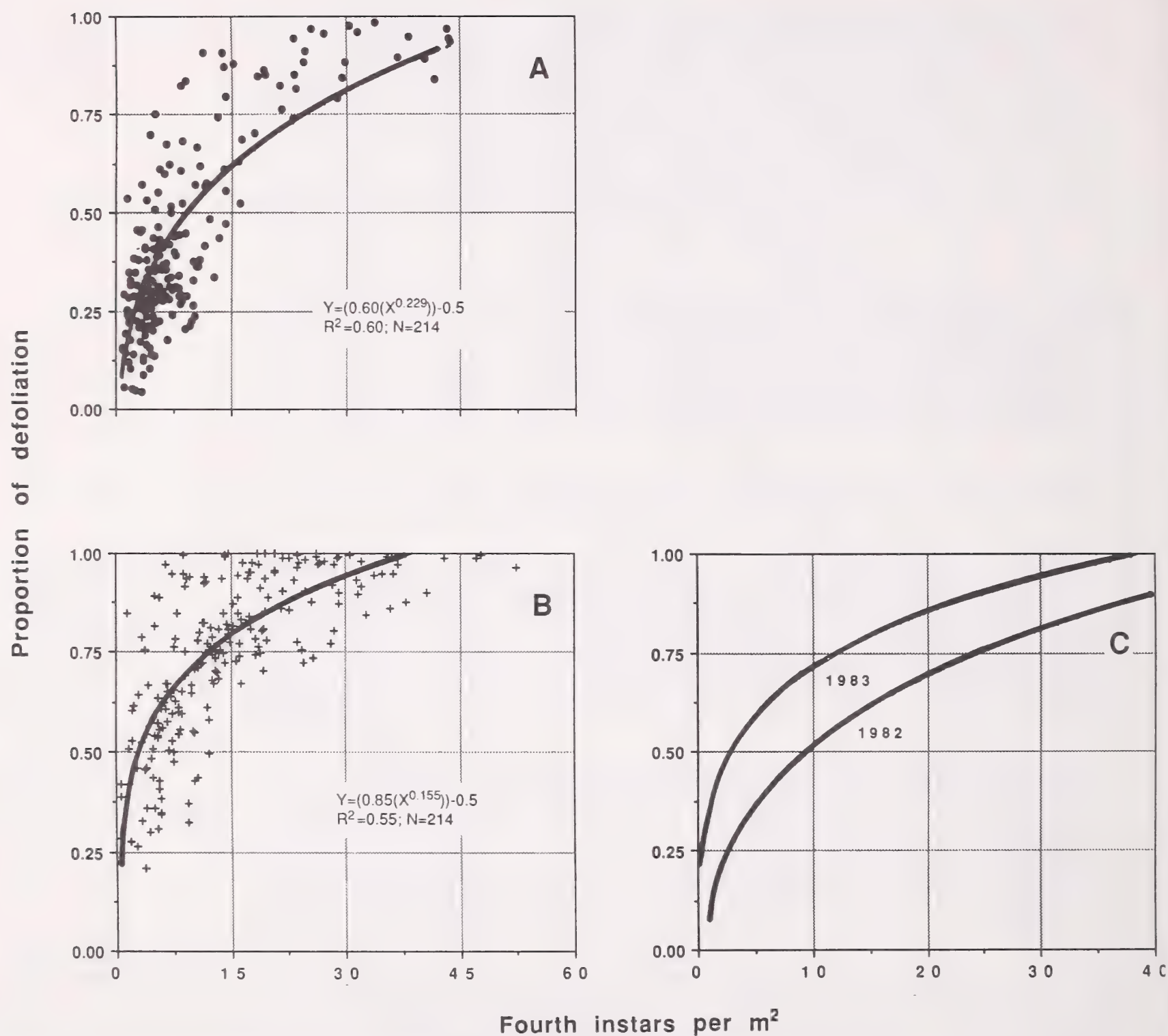
Figure 17—Fourth-instar density and subsequent defoliation in MONT: A, 1982; B, 1983; C, comparison, 1982 and 1983.

4.4.3.7 Influence of stand—In western Montana, in mixed stands of Douglas-fir and ponderosa pine, *Pinus ponderosa* Dougl. ex Laws., defoliation of Douglas-fir increased as the percentage of Douglas-fir increased (Fauss and Pierce 1969). Similarly, defoliation in both IDA and MONT (tables 21-22) shows the same pattern.

Several investigators in northwestern forests have found that the true firs (grand fir, subalpine fir, or both species) sustained heavier defoliation than either Engelmann spruce or Douglas-fir (Carolin and Coulter 1975, Stoszek and Mika 1985, Williams 1966, Williams and others 1971). And in the Southwest, Parker and others (1979) found that white fir was
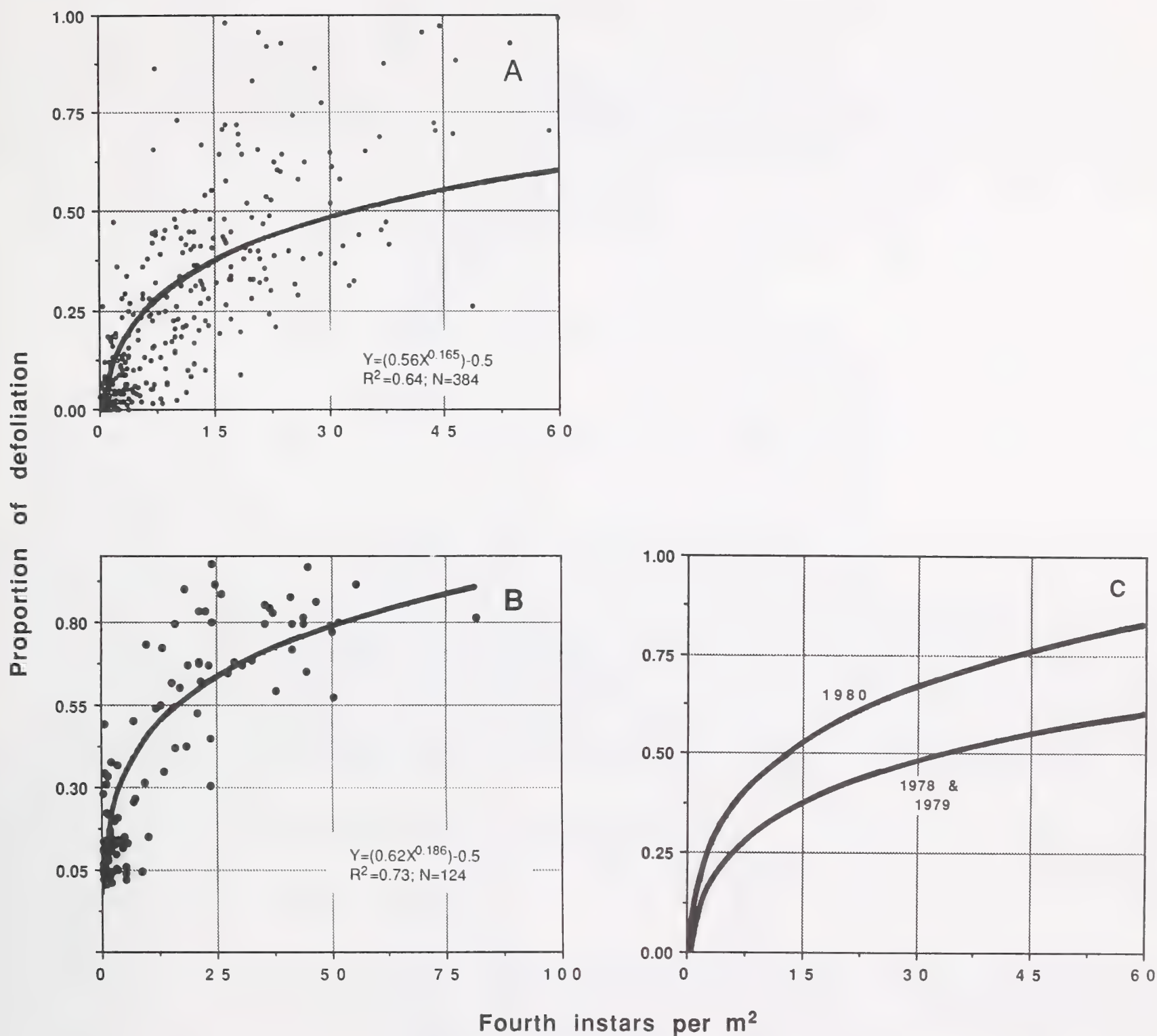
Figure 18—Fourth-instar density and subsequent defoliation in NMEX: A, 1978 and 1979; B, 1980; C, comparison, 1980 and other years.

more heavily defoliated than Douglas-fir. Results derived and presented here (figs. 25 and 26) support these findings in both the Northwest and the Southwest.

Schmidt and others (1983) stated that "...apparent budworm 'feeding preference' is in the same approximate order as shade tolerance of the trees—the most shade-tolerant species are fed on most heavily." Using this relation, several authors rank the true firs as most defoliation-prone, followed by Engelmann spruce and Douglas-fir, in that order (Carlson and others 1985a, Carlson and Wulf 1989, Schmidt and others 1983, Wulf and Cates 1987). For mixed stands in IDA, the results are somewhat equivocal; they show

67
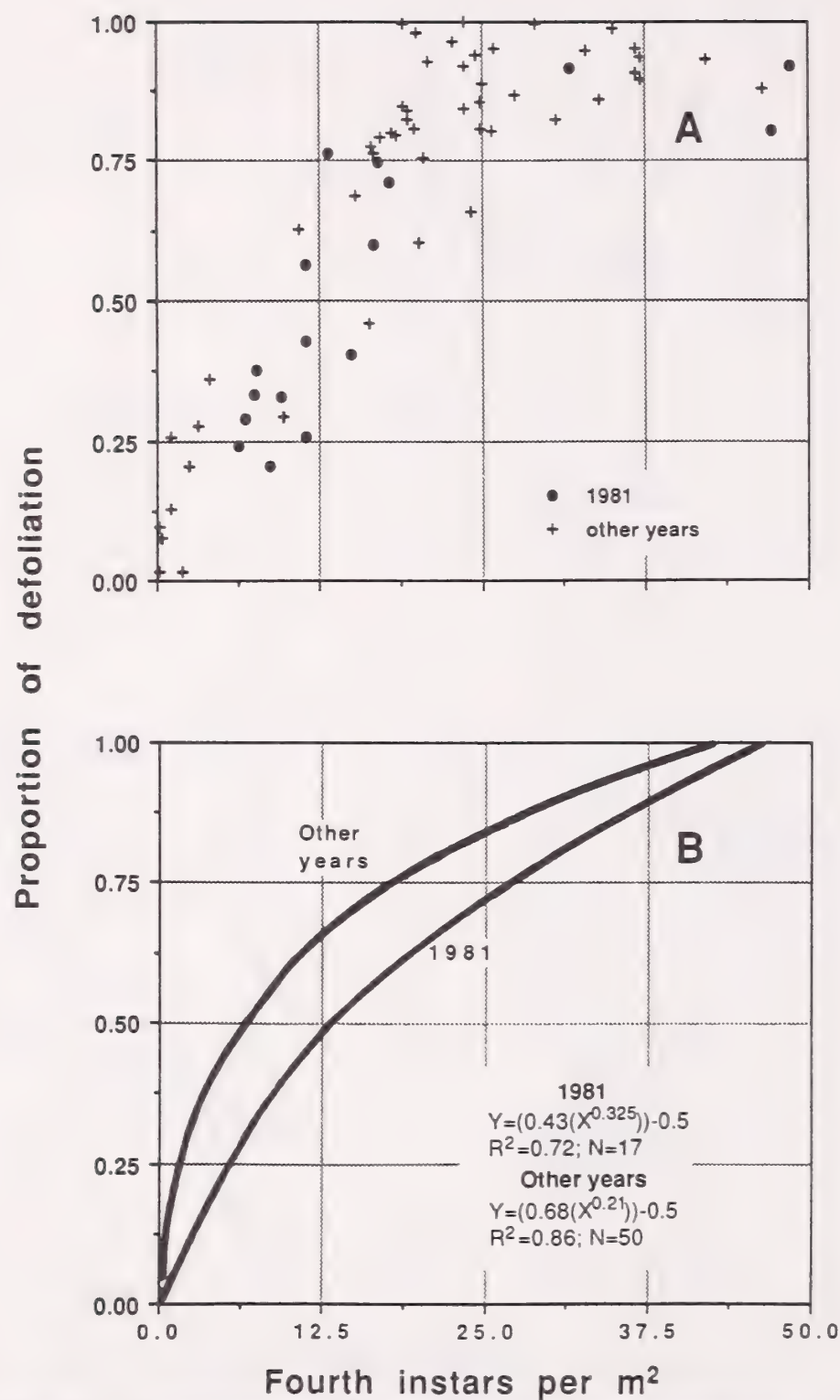
Figure 19—Fourth-instar density and subsequent defoliation in DAMAG: A, scatter diagram, 1981 and other years; B, comparison, 1981 and other years.

that defoliation and the proportion of the overstory foliage in all of the host species (DOUG, TRUE, and SPR) tended to increase together (table 21). For mixed stands in NMEX, however, the results show a consistent inverse relation between defoliation and the proportion of spruce foliage in the overstory (table 23, fig. 27). Implications arising from these findings are discussed in section 5.3.1.

Garton and others (1985) note that "The shrub layer appears to be particularly important to many of the birds that feed on budworm." Consequently, Takekawa and others (1982)
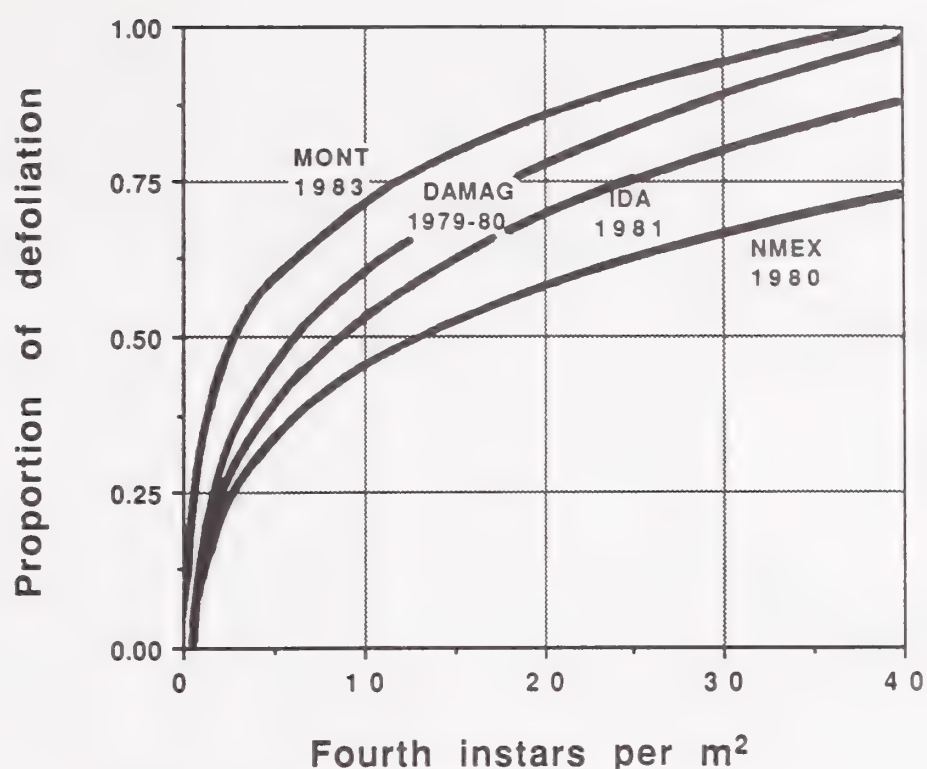
Figure 20—Fourth-instar density and proportion of defoliation in IDA (1981), MONT (1983), NMEX (1980), and DAMAG (1978-79).

and Langelier and Garton (1986) include practices to maintain or enhance shrub under-stories among their recommendations for increasing populations of insectivorous birds. Based on this recommendation, one might expect an inverse relation between high shrub density and defoliation. Unfortunately, the results I derived are not completely consistent. High shrub density was associated with lower than expected defoliation in the relatively moist sites in both IDA (at all densities) and NMEX (at high densities). For example, here are mean values of percentage of defoliation in IDA as a function of shrub density:

Plot category	Number of plot-years	Mean percent defoliation	Standard error
High shrub density	109	37.9	2.71
Other	206	45.3	2.03

High shrub density, however, was also associated with higher than expected defoliation in the chronically droughty sites in MONT (at low densities). This inconsistency suggests that budworm-related management practices designed, in part, to increase shrub density should not be applied in locations where moisture is clearly a principal limiting factor.

**4.5
Projecting Emerging
Moths**

**4.5.1
The Equations**

4.5.1.1 COLO, PNW, and SAMP—Densities of residual pupae (N_p), rather than emerging moths (N_A), were estimated among the populations in SAMP. For this reason, this analysis uses N_p rather than N_A, as the dependent variable. From procedures described in section 3.4.5, the following equation (44) was derived for relating N_p to underlying conditions in situations similar to those encountered in COLO, PNW, and SAMP:

$$N_p = 0.0818 N_L^{1.353} \cdot [1.0 - 0.00542 N_L] \cdot WET^{-.614} \cdot VCD^{1.665}. \qquad (44)$$
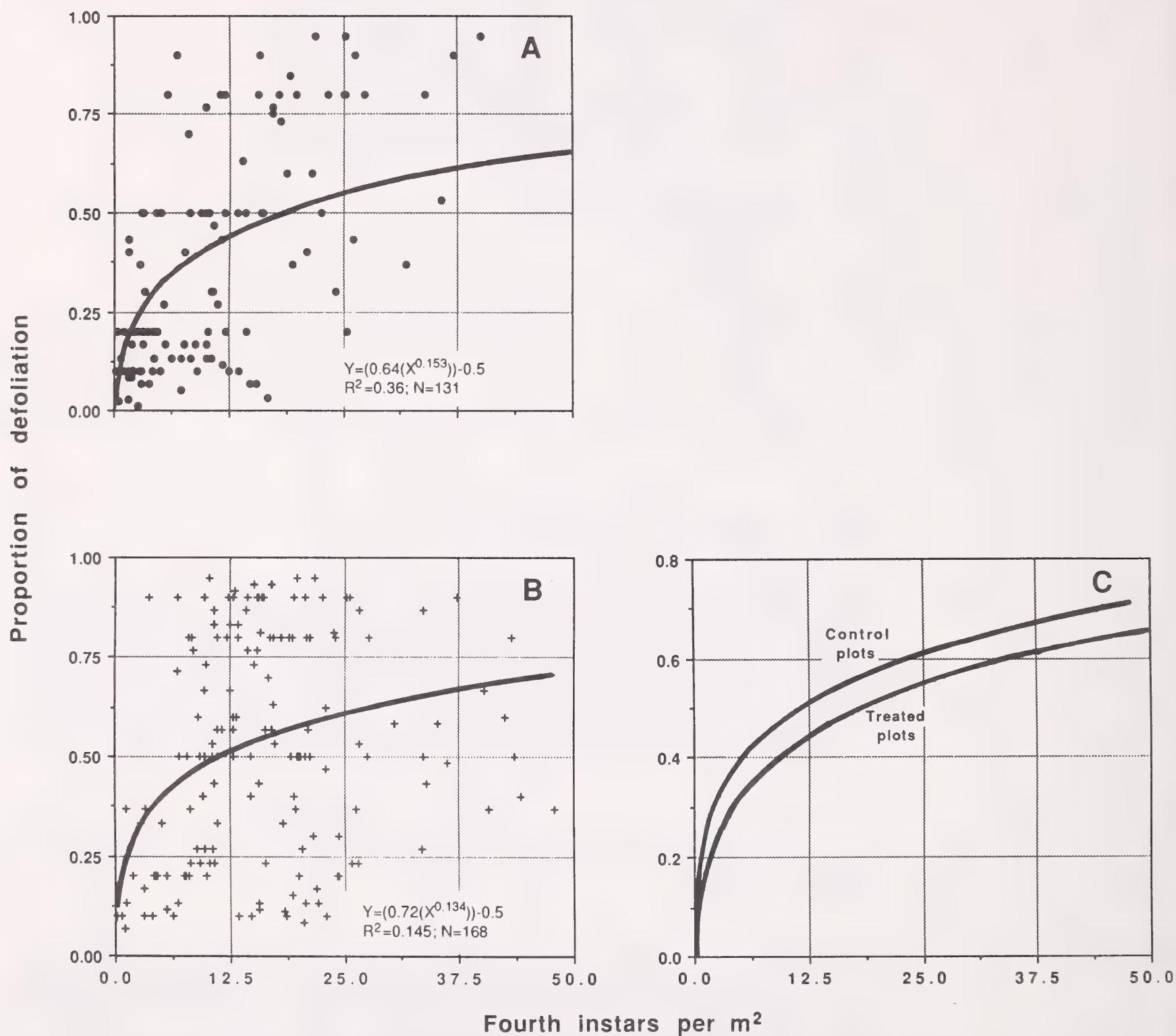
Figure 21—Insecticide treatment and the relation between fourth-instar density and defoliation during subsequent years in IDA: A, treated plots; B, control plots; C, comparison, treated and control plots.

4.5.1.2 OREG—The following equation (45) was derived for relating N_A to N_L and YRIDX, in conditions similar to those encountered in OREG:

Year is similar to 1982-85:
$$N_A = 0.117N_L^{1.369} \cdot [1-0.0058N_L] .$$ (45A)

Year is similar to 1986-88:
$$N_A = 0.060N_L^{1.369} \cdot [1-0.0058N_L] .$$ (45B)
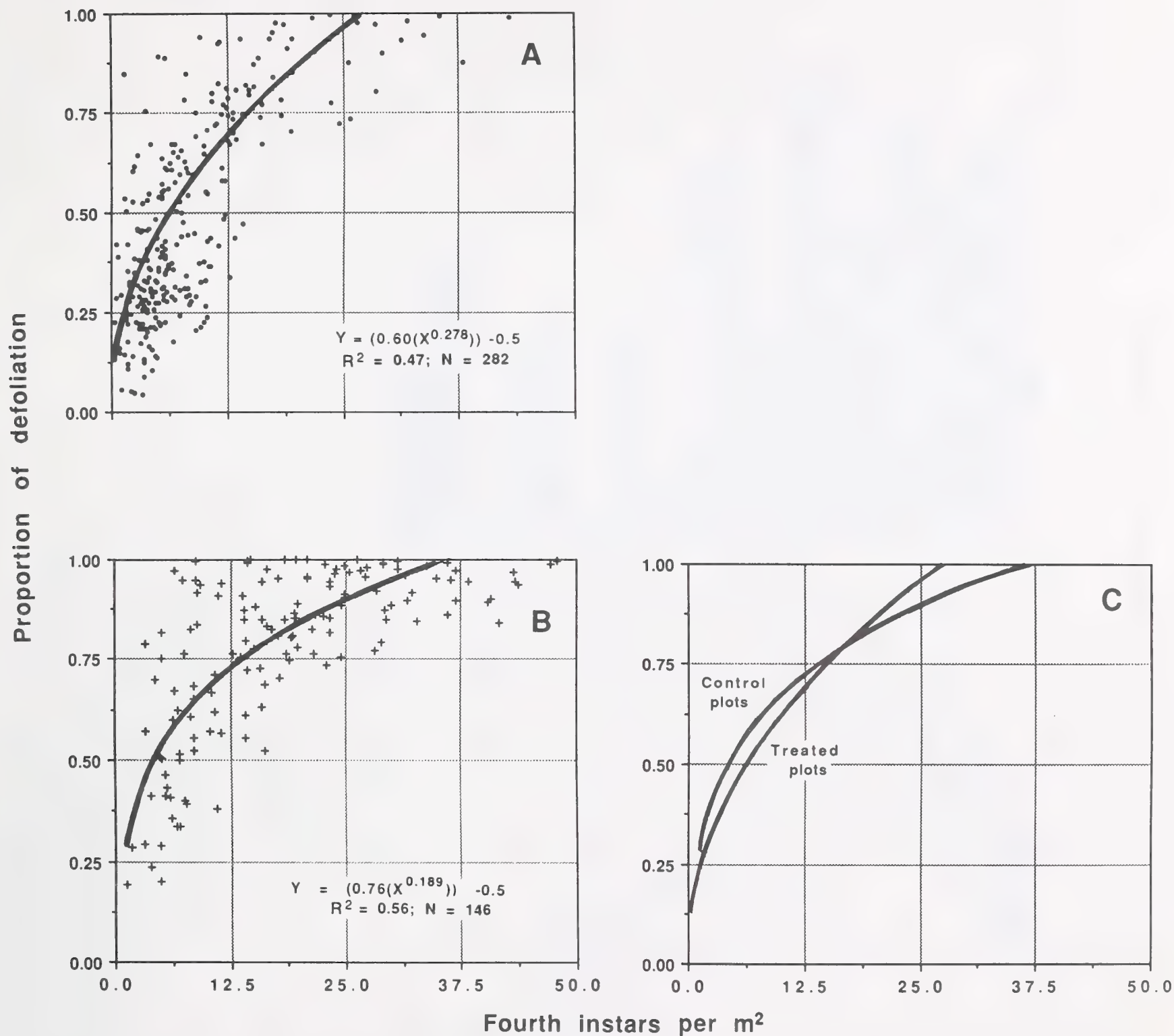
Figure 22—Insecticide treatment and the relation between fourth-instar density and defoliation during subsequent years in MONT: A, treated plots; B, control plots; C, comparison, treated and control plots.

**4.5.2
Influence of Predators**

Estimates of predation on the western budworm were derived from two kinds of trials. First, we routinely used pupae collected from nearby populations by clipping twigs containing individual pupae. These twigs were then wired to branches in the populations under study (Campbell and others 1982, Campbell and Torgersen 1982, Torgersen and Campbell 1982). Generally, only one pupa was wired to any given branch. Periodically, however, we experimented with higher densities. In most such cases, ensuing pupal mortality rates were directly related to the number of pupae per branch.
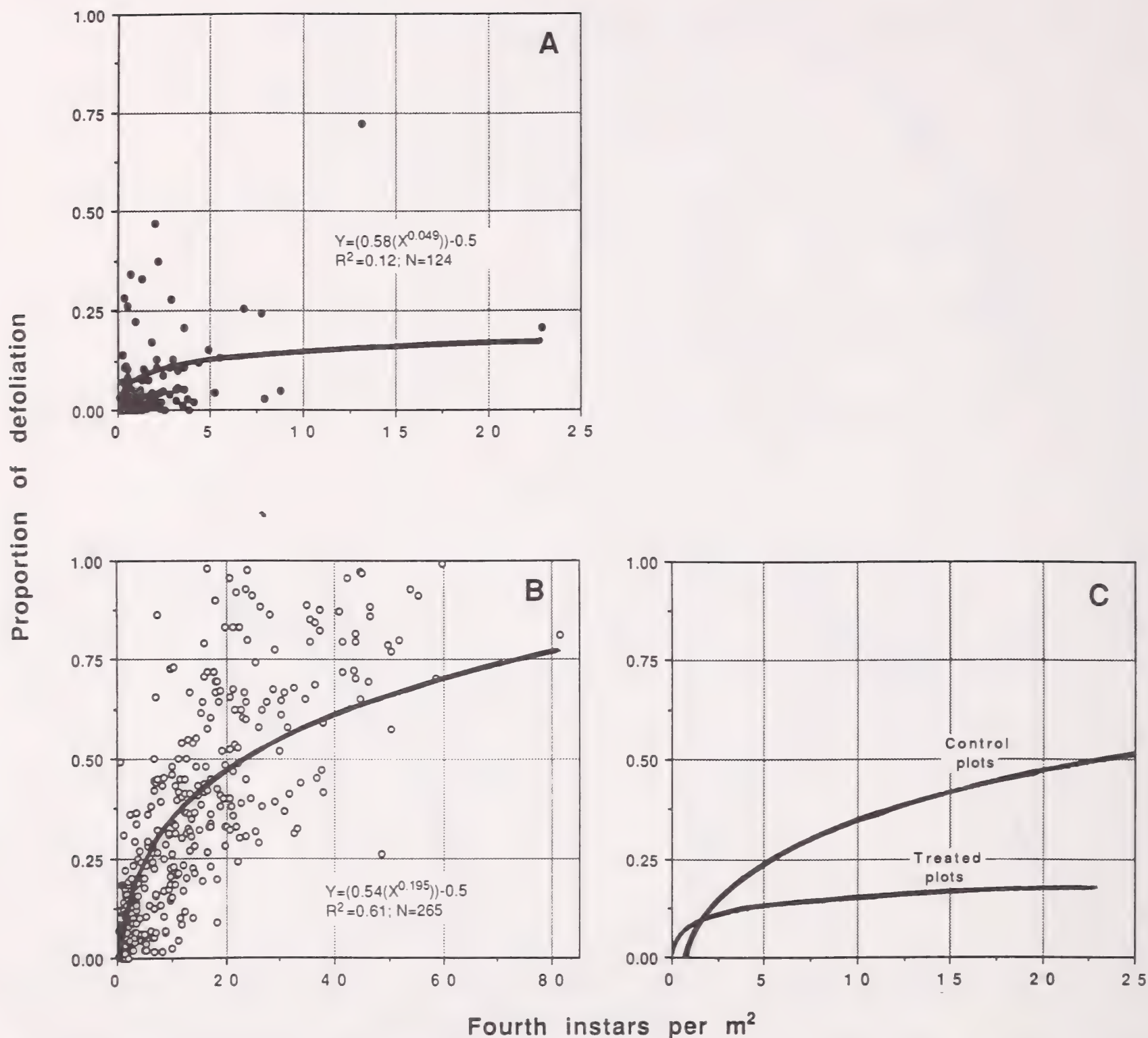
Figure 23—Insecticide treatment and the relation between fourth-instar density and defoliation during subsequent years in NMEX: A, treated plots; B, control plots; C, comparison, treated and control plots.

Second, we used exclosures. Campbell and others (1983b) used the results derived during 1980 from whole-tree exclosures and sticky barriers to show that up to 15 times as many adult moths were produced on trees protected from both birds and ants as on control trees. In 1981, the exclosure study was continued in plots in eastern Oregon and western Montana. Combined results from this 2-year study are shown in figure 28.

**4.5.3
Relations Specified
by the Results**

4.5.3.1 Density dependence— The relation between N_L and survival from N_L to N_P among the 59 observations drawn from COLO, PNW, and SAMP is shown in figure 29. For densities between about 1 and 50 larvae per m^2, S_L and N_L increased together.
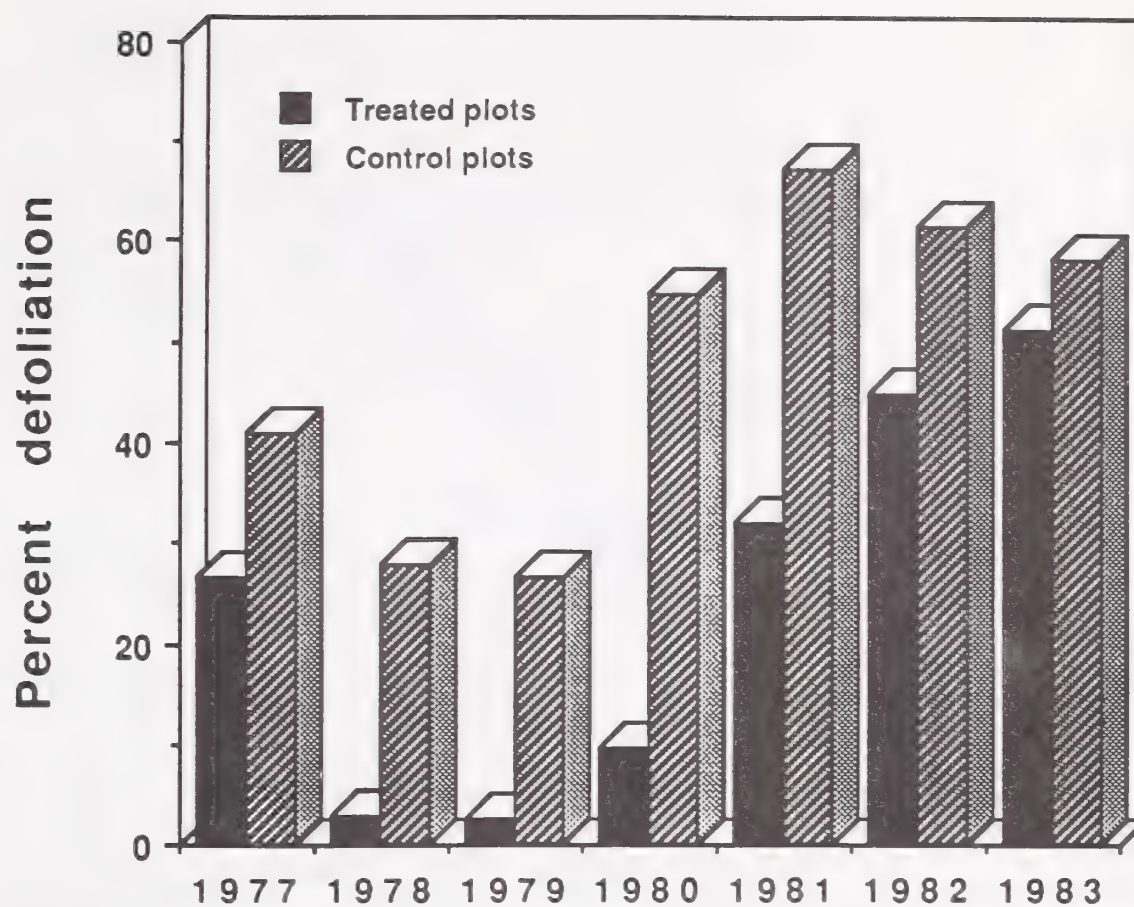
Figure 24—Defoliation in treated and control plots in NMEX, 1977 (treatment year) through 1983 (from Telfer 1984).
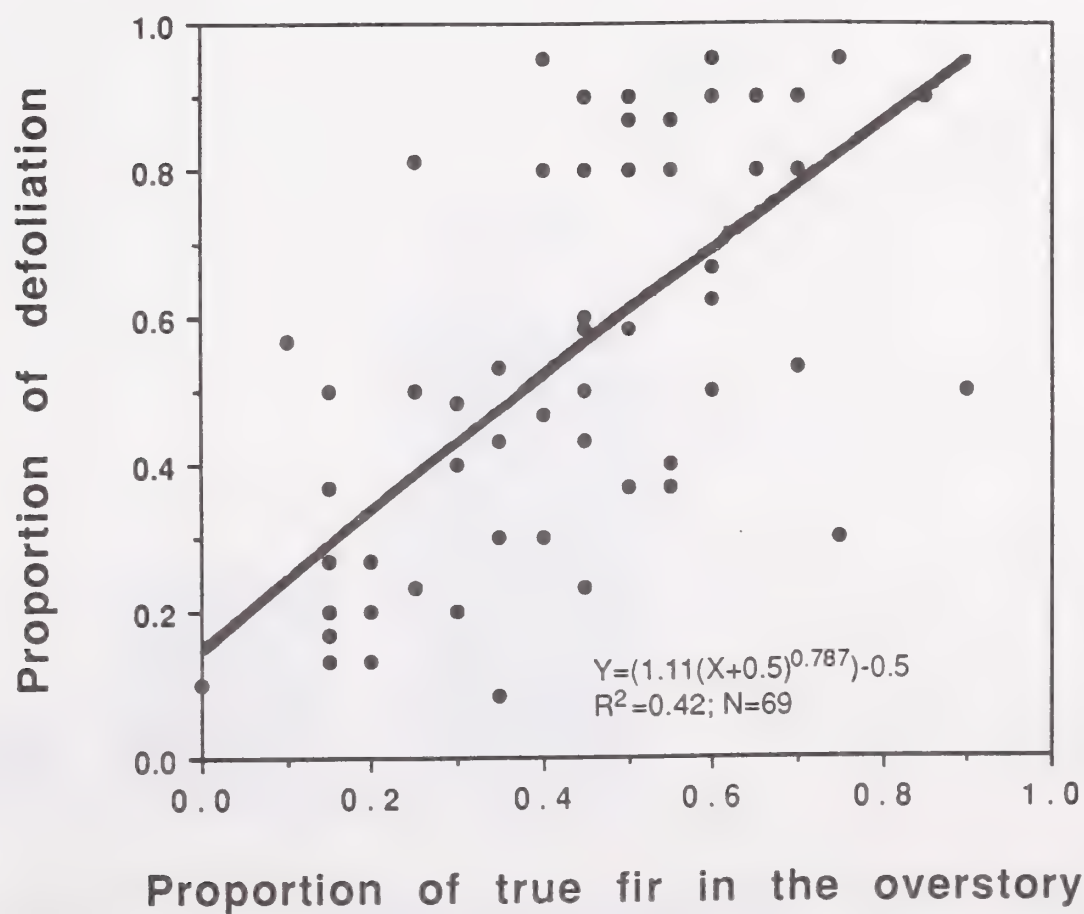
Figure 25—Proportion of the overstory foliage in true fir and defoliation in IDA; N_L > 20 per m².
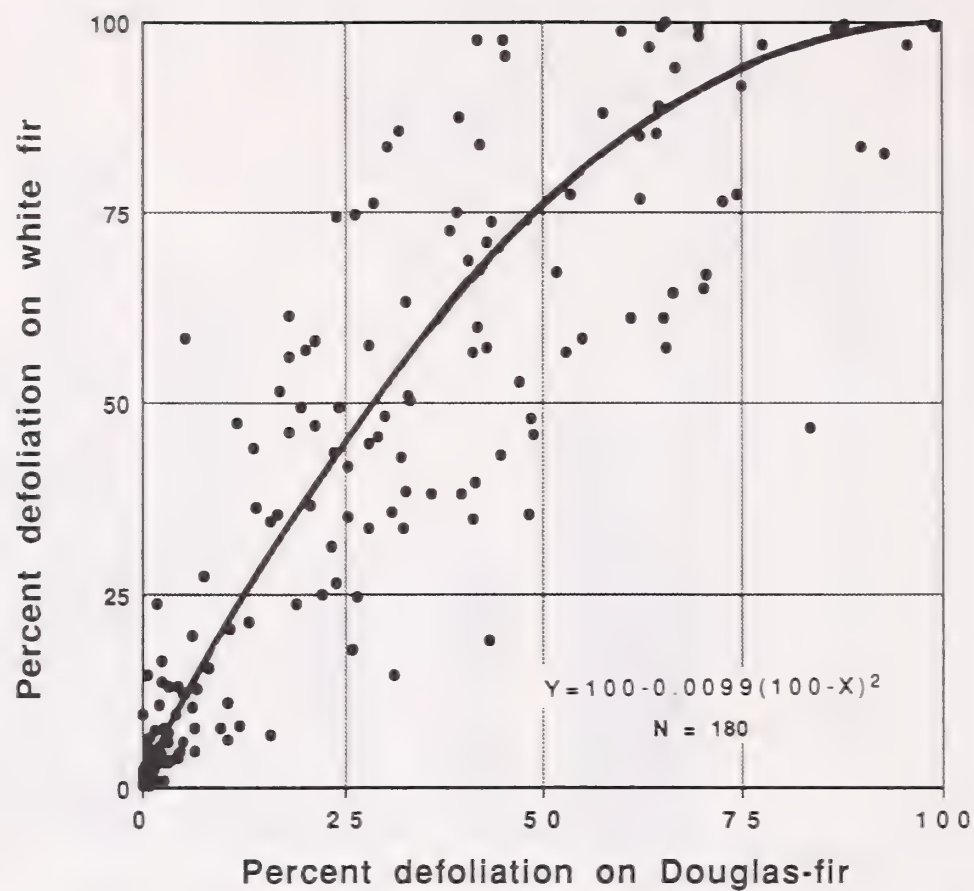
Figure 26—Defoliation on white fir as a function of defoliation on Douglas-fir in NMEX.

$$Y = 100 - 0.0099(100 - X)^2$$

$$N = 180$$
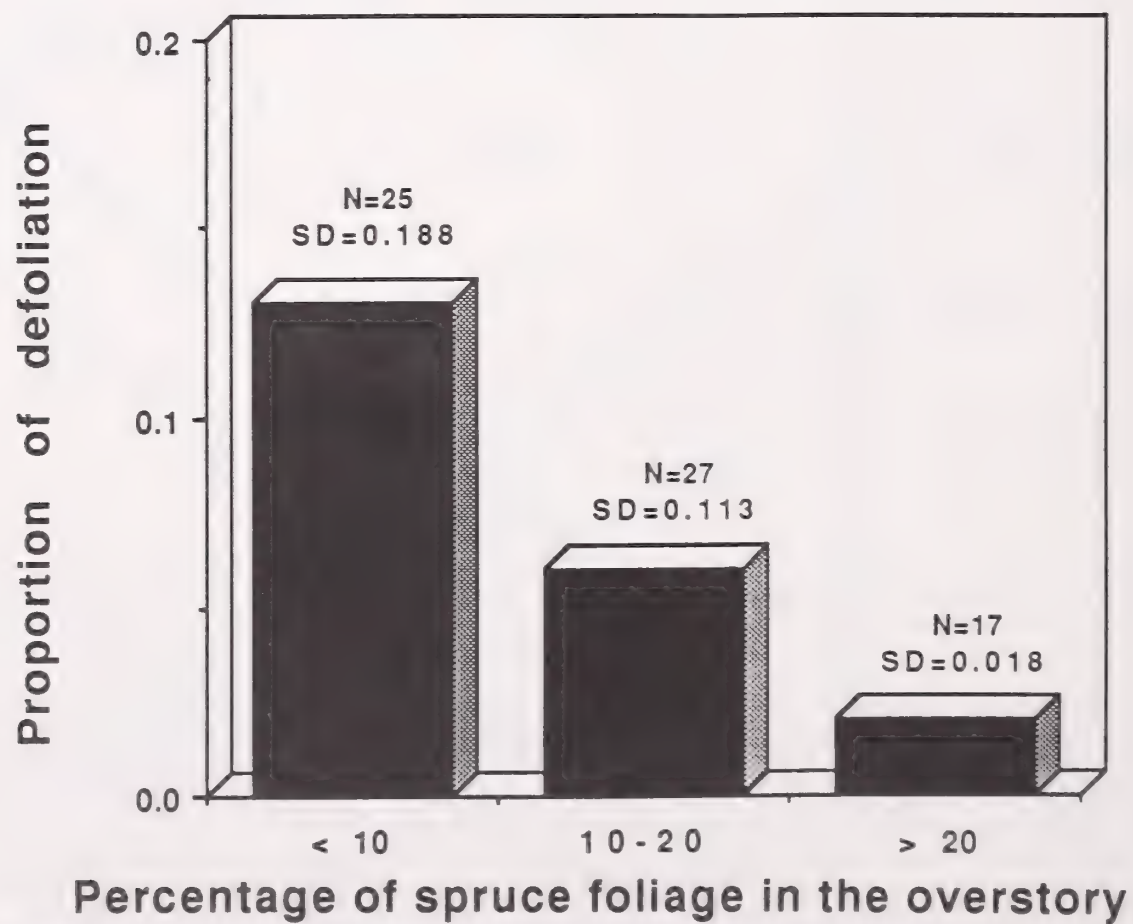
Figure 27—Proportion of the overstory foliage in spruce and defoliation in NMEX; no more than four fourth instars per m².
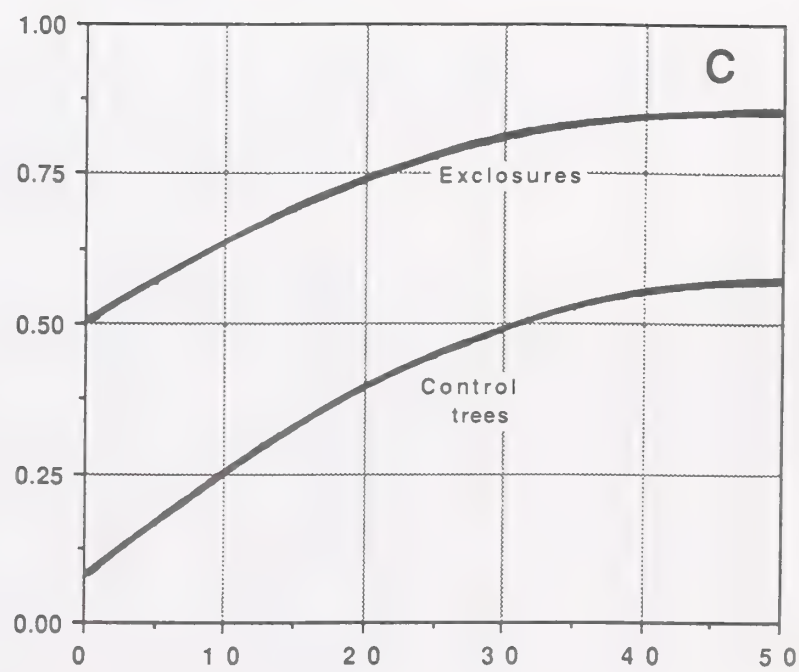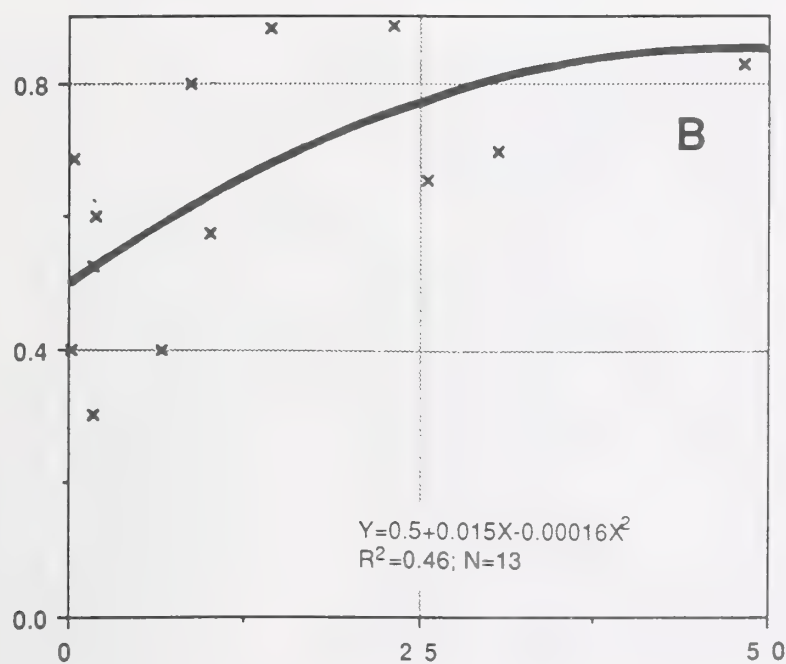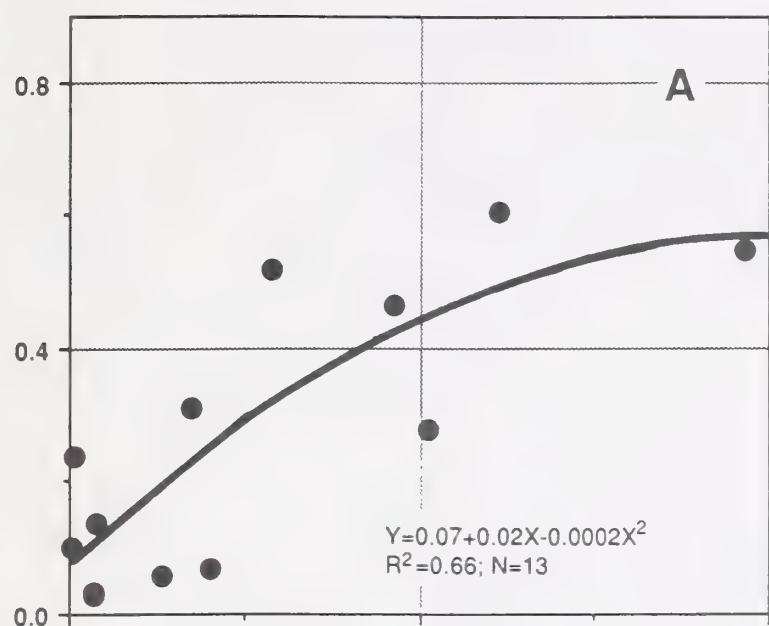
Figure 28—Survival rates from nominal fourth instar to emerging moths on trees where birds and ants were excluded, and on control trees, in PNW: A, control trees; B, trees with birds and ants excluded; C, comparison, control trees and in exclosures.

Survival began to decline as N_L continued to increase above about 50 larvae per m², and the population may collapse if N_L continues to increase above about 150 larvae per m². Mortality-causing processes thought to be responsible for this numerical pattern are discussed in section 5.2.1.

4.5.3.2 Differences across years—Late survival (S_L) systematically declined from year to year as the outbreak in OREG progressed (fig. 30). According to Torgersen (1988), most of the OREG plots were heavily defoliated for the first time in either 1984 or 1985. By 1986, the data reflect a substantial decline in S_L, which continued through 1988.

$Y = 0.074X^{0.353} (1. - 0.0054X)$
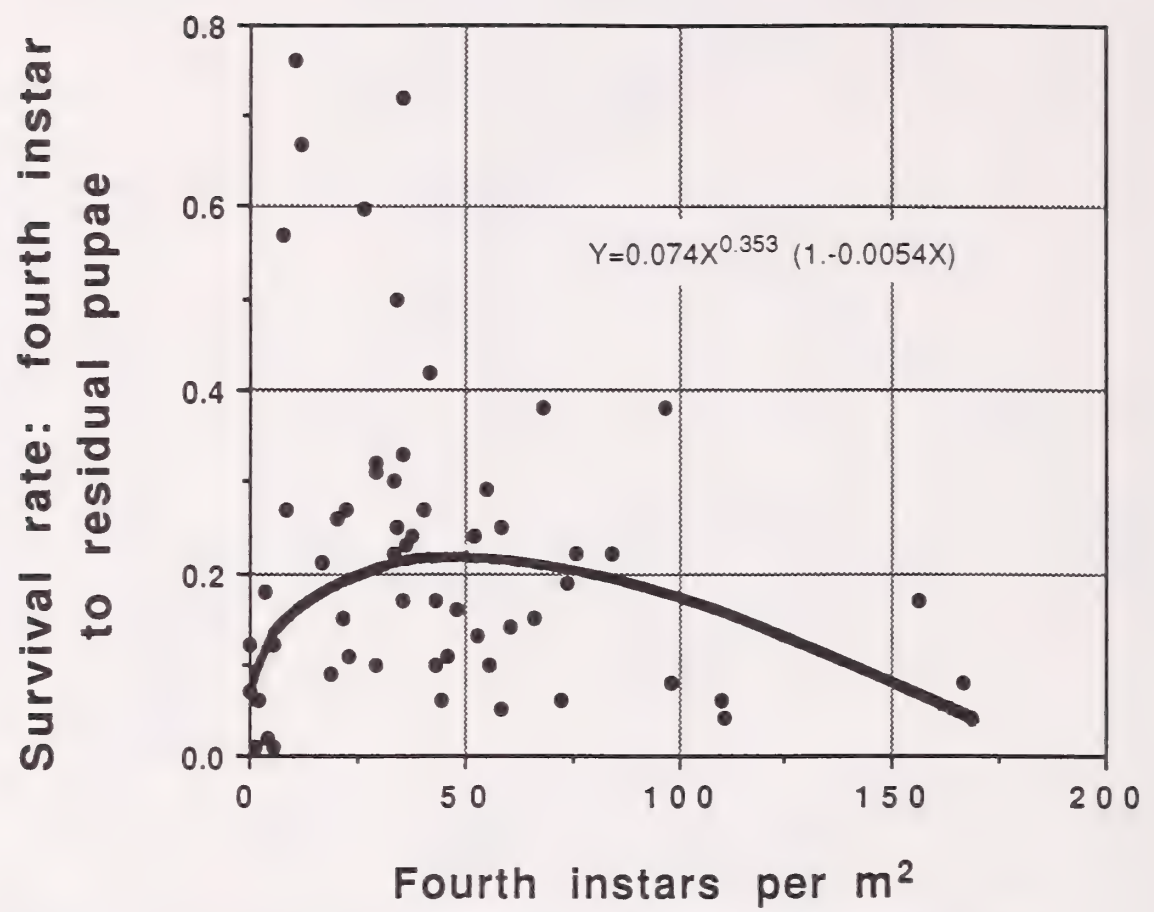
Figure 29—Fourth-instar density and survival to residual pupae in COLO, PNW, and SAMP.
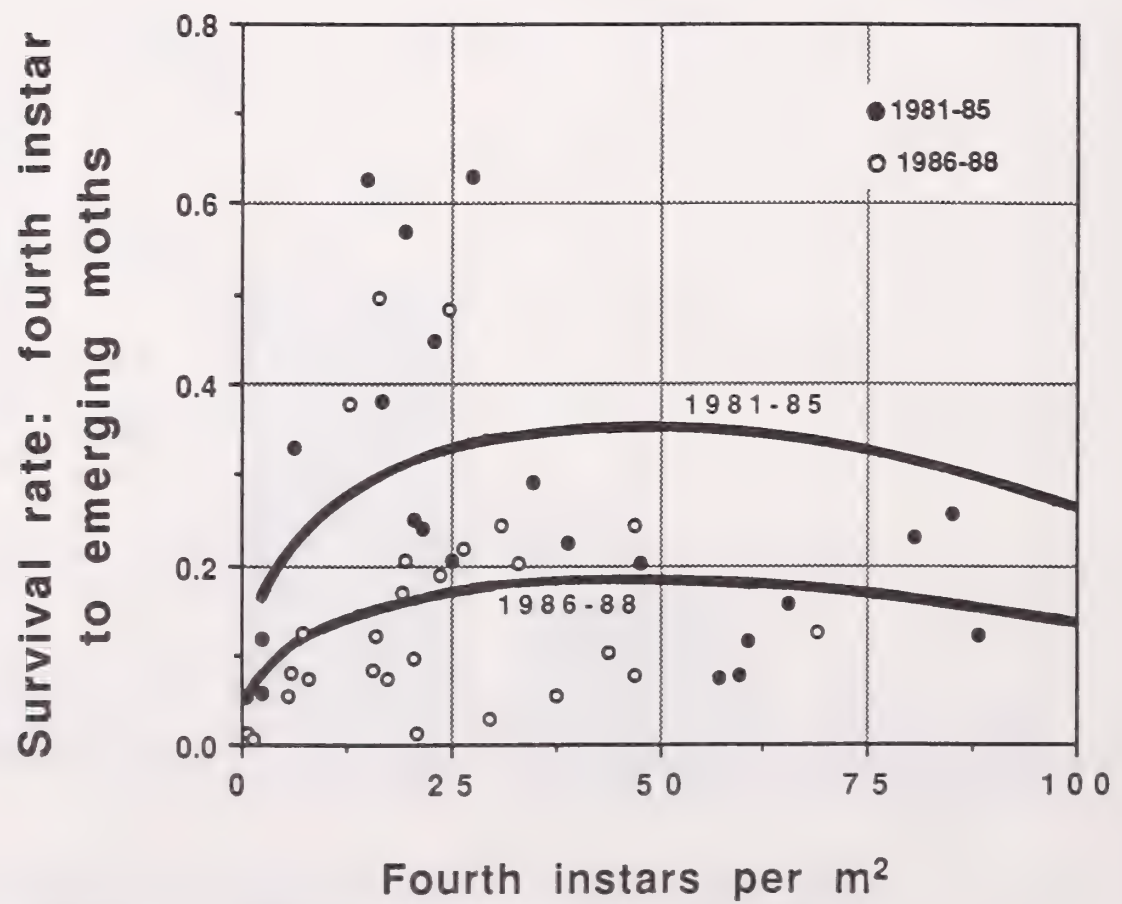
Figure 30—Fourth-instar density and survival to emerging moths in OREG.

Underlying processes that may be implied by this systematic year-to-year decline in S_L are discussed in sections 5.2.1 and 5.2.3.

4.5.3.3 Influence of site—An inverse relation was found between S_L and site wetness in the COLO, PNW, and SAMP plots (equation 44). The mean values of S_L among the populations on wet sites and drier sites in COLO, PNW, and SAMP are as follows:

Plot category	Number of plot-years	Mean S_L	Standard error
Wet sites	18	0.124	0.032
Other	41	.258	.028

Many authors (for example, Fauss and Pierce 1969, Fellin and others 1983, Williams and others 1971) have reported that defoliation is lower in stands growing on wetter sites, and both Kemp (1985) and Hard and others (1980) found inverse correlations between precipitation and defoliation. Wulf and Cates (1987) reviewed several processes that have been proposed to explain the inverse correlation between budworm density and site wetness. To add to that list, riparian corridors doubtless attract a diverse and abundant bird community in interior western forests (Langelier and Garton 1986, Thomas and others 1979). By extension, the average density of avian predators in these same forests should be directly related to site wetness.

4.5.3.4 Influence of stand—Analysis of the COLO, PNW, and SAMP data revealed a positive relation between S_L and variation in crown depth (equation 44). Particularly across densities below about 10 fourth instars per m², S_L was about twice as high in stands with above average variation in crown depth.

Morris (1955) noted that most of the larger eastern budworm larvae that dropped to the understory were eaten by white-footed mice, *Peromyscus leucopus* Rafinesque. Similarly, Campbell and others (1984c) found that birds and ants severely reduced survival of both late instars and pupae of the western budworm on seedlings in western Montana. Further, casual but repeated observations suggest that the half-life of late-instar western budworms that drop to the forest floor can often be measured in minutes. For example, Silver (1960) in British Columbia reported that the foraging ant, *Camponotus vicinus* Mayr, "...in 40 to 45 minutes... removed 40 per cent of 241 [budworm] larvae placed on a beating sheet." These observations both support Wulf and Cates' (1987) conclusion that "multistoried stands are generally more susceptible than single-storied ones of the same host species because of the inevitable downward drift of large larvae" and suggest a likely fate for larvae that drop to the forest floor.

**4.6
Projecting Egg Masses**

**4.6.1
Calculating the Density
of Emerging Moths**

Densities of emerging moths (N_A) were not observed in IDA, MONT, NMEX, or DAMAG. In each of these areas, values of N_A were calculated from a modified version of equation (44)—the equation developed from the COLO, PNW, and SAMP data. In that equation, the density of residual pupae (N_P) is projected as a function of N_L and two environmental attributes (WET and VCD). To project N_A in IDA, MONT, NMEX, and DAMAG, this equation was modified in two ways. First, the two environmental attributes (WET and VCD) were ignored. This step eliminated the possibility of introducing a systematic bias in the resulting estimate of N_P as a function of one or both of these untested variables. Second, to obtain values of N_A, the projected values of N_P were multiplied by 0.9, the average survival rate found for the interval from residual pupae to emerging moths (N_A/N_P) in Idaho (Campbell and others 1984a). Thus, the equation used in these projections is as follows:

$$N_A = 0.07362N_L^{1.353} \cdot [1.0 - 0.00542N_L] . \tag{46}$$

To avoid underestimating N_A at low densities, values of N_A below $N_L = 1$ per m² were calculated as $N_A = 0.09N_L$. Mean, minimum, and maximum calculated values of N_A in each of the above areas are shown in table 5 (p. 16).

Unfortunately, the equation used to generate N_A may have introduced a systematic bias toward high survival, at least for the plots in the above areas. This equation is based on the numerical behavior of the budworm during suboutbreaks (the PNW data), and two new outbreaks, SAMP and COLO. It does not explicitly consider the depressing effect of an extended outbreak on S_L that was found in OREG (section 4.5.1.2). Consequently, the equation may overestimate N_A during the prolonged outbreak conditions that were present in IDA, MONT, and NMEX. Fortunately, the principal effect of this bias, if it occurred, would merely be a subsequent underestimate in the parameters to be derived in this section that will relate N_A to subsequent N_M.

4.6.2
The Equations

4.6.2.1 IDA(1)—These analyses, which include indices of interstand influences (SIZ and DST), use 414 plot-years derived from IDA. When the model (29) was tested, 11 statistically significant variables were identified (table 24). Five of these variables, each significant beyond $p = 0.001$, were associated with most of this same variation. These five variables entered the reduced model as follows:

Step	Variable	R^2
1	$\ln N_A$	0.315
2	$(\ln SIZ_{(n)} \cdot \ln YR2)$	.360
3	$\ln DOUG$	.392
3	$(\ln SIZ_{(n)} \cdot \ln YR2)$ replaced by $\ln YR2$	.392
4	$\ln WET$	.411
5	$\ln SIZ_{(n)}$	.425
5	$\ln WET$ replaced by $\ln YR3$	.427

4.6.2.2 IDA(2)—This IDA (2) analysis, using model (31), does not include indices of interstand influences. In this test, nine statistically significant variables were identified. Most of the variation associated with these variables was also associated with a reduced set of four variables (table 24), each of which is significant beyond $p = 0.001$. These four variables are as follows:

Step	Variable	R^2
1	$\ln N_A$	0.315
2	$\ln YR2$	.351
3	$\ln DOUG$	.392
4	$\ln WET$	.411

4.6.2.3 MONT—These analyses use the 426 plots-years in MONT that include estimates of both N_A and N_M. Nine statistically significant variables were identified; three, each significant beyond $p = 0.001$, were associated with most of the same variation in $\ln N_M$ (table 25). Here are the three variables in the reduced model:

Step	Variable	R²
1	$(\ln N_A \cdot \ln YR2)$	0.218
2	$\ln YR3$	.252
3	$\ln AGE$	.271
3	$\ln YR3$ replaced by $\ln N_A$	.275
3	$(\ln N_A \cdot \ln YR2)$ replaced by $(\ln N_A \cdot \ln YR3)$	.277

4.6.2.4 NMEX—Ten variables were related to the variation in $\ln N_M$ in the NMEX test; four, each significant beyond $p = 0.001$, were associated with almost all of this same variation (table 26). Here are the four variables, in their order of appearance:

Step	Variable	R²
1	$\ln N_A$	0.521
2	$\ln YR4$	.608
3	$\ln TRT$	.626
4	$\ln YR3$	.639

Table 24—Regression coefficients for estimating egg masses ($\ln N_M$); data from IDA; N = 414

Variable	Model (29) (includes lnSIZ and lnDST) Full	Reduced	Model (31) Full	Reduced
Intercept[a]	0.939	1.690	-0.665	1.730
$\ln SIZ_{(n)}$	ns[b]	1.086	--	--
$(\ln SIZ_{(n)} \cdot \ln YR2)$	2.100		--	--
$\ln DST_{(n)}$	-.287		--	--
$(\ln DST_{(n)} \cdot MED)$	2.306		--	--
$(\ln DST_{(n)} \cdot HI)$	4.161		--	--
$\ln N_A$	.315	.426	.301	.470
$(\ln N_A \cdot \ln YR3)$	.244		ns	
$\ln YR2$	ns	-.497	-.789	-.766
$\ln YR3$	ns	.507	ns	
$(\ln TRT \cdot LO)$	-.943		-.735	
$(\ln TRT \cdot HI)$	.594		.363	
$\ln ELEV$	ns		.824	
$\ln WET$	ns		-.323	-.429
$\ln DOUG$	1.408	1.374	.799	1.207
$(\ln TRUE \cdot MED)$	.866		ns	
$(\ln TRUE \cdot HI)$	ns		-.871	
$\ln SPR$	-1.023		-.880	
R^2	.501	.427	.451	.411
RTMSE	.906	.963	.948	.975

[a] Intercept corrected for logarithmic bias.
[b] Not significant.

Table 25—Regression coefficients for estimating egg masses (lnN$_M$) using model (30); data from MONT; N = 426

Variable	Full model	Reduced model
Intercept[a]	2.720	3.840
lnN$_A$	.301	.393
(lnN$_A$ · lnYR3)	-.296	-.320
lnEL3	.182	
lnEL4	.304	
(lnSLOPE · HI)	-1.101	
(lnSASP · LO)	-.536	
lnWASP	-.417	
lnDOUG	2.531	
lnAGE	-.465	-.522
R^2	.354	.277
RTMSE	.594	.624

[a] Intercept corrected for logarithmic bias.

Table 26—Regression coefficients for estimating egg masses (lnN$_M$) using model (31); data from NMEX; N = 357

Variable	Full model	Reduced model
Intercept[a]	1.751	2.018
lnN$_A$	.391	.521
lnYR3	.388	.398
lnYR4	1.221	1.173
lnTRT	-1.104	-.556
(lnTRT · LO)	.734	
EL5	-.786	
lnPROD	.439	
(lnPROD · LO)	-.646	
lnSPR	-2.306	
(lnVCD · MED)	.669	
R^2	.677	.639
RTMSE	.803	.841

[a] Intercept corrected for logarithmic bias.

4.6.2.5 DAMAG—To test model (32), I used the 66 plot-years that included estimates of both N_A and subsequent N_M. Five variables were significant in this model, and were associated with about 54 percent of the variation in lnN_M. Here are the five variables, in their order of entry:

Step	Variable	R^2
1	lnEL5	0.290
2	lnN_A	.382
3	lnYR2	.460
4	lnDOUG	.502
5	lnYR1	.542

Here is the relation between N_M and these variables (equation 47):

Year is similar to 1979:
$$N_M = 24.9N_A^{.220} \cdot EL5^{-.847} \cdot DOUG^{-.643} . \qquad (47A)$$

Year is similar to 1980:
$$N_M = 31.3N_A^{.220} \cdot EL5^{-.847} \cdot DOUG^{-.643} . \qquad (47B)$$

Year is similar to 1981 or 1982:
$$N_M = 16.7N_A^{.220} \cdot EL5^{-.847} \cdot DOUG^{-.643} . \qquad (47C)$$

4.6.2.6 COLO and PNW—To test model (33), I used the 40 plot-years from the combined COLO-PNW data set that included estimates of both N_A and N_M. Two variables were significant, and they were associated with about 81 percent of the variation in lnN_M ($R^2 = 0.809$):

Step	Variable	R^2
1	lnN_A	0.759
2	(lnVCD · PNW)	.809

The analysis specifies the following relation between N_M and these variables (48).

If area is similar to PNW:
$$N_M = 2.6N_A^{.579} \cdot VCD^{2.029} . \qquad (48A)$$

If area is similar to COLO:
$$N_M = 2.6N_A^{.579} . \qquad (48B)$$

4.6.2.7 OREG—For this OREG analysis (model 34), I used the 49 plot-years in Oregon that included estimates of both N_A and N_M. Here are the significant variables, in their order of entry in the model:

Step	Variable	R^2
1	lnN_A	0.542
2	lnYR7	.593

The relation between N_M and these variables is as follows (49):

Year is similar to 1988:
$$N_M = 1.56N_A^{.530}.$$
(49A)

Other years:
$$N_M = 3.71N_A^{.530}.$$
(49B)

4.6.2.8 WXBASE—To test model (35), I used the 193 plot-years from WXBASE that included successive estimates of N_M, an estimate of outbreak size (SIZ) at the start of generation (n), and an estimate of precipitation during May, June, and July (PCP3). Seven variables were significantly associated with $N_{M(n)}$ and were entered in the model in the following order:

Step	Variable	R^2
1	$lnN_{M(CALC)}$	0.497
2	$lnDEF_{(n)}$	.592
3	lnPCP3	.608
4	$(lnSIZ \cdot lnYR3)$	.619
5	$(lnSIZ \cdot lnYR8)$	.630
6	$(lnSIZ \cdot lnYR5)$	.640
7	lnSIZ	.649

Equation (50) describes the relation found between $N_{M(n)}$ and these variables:

Year is similar to 1963:
$$N_M = 0.45N_{M(CALC)}^{.422} \cdot DEF^{.705} \cdot PCP3^{.565} \cdot SIZ^{-.787}.$$
(50A)

Year is similar to 1965:
$$N_M = 0.45N_{M(CALC)}^{.422} \cdot DEF^{.705} \cdot PCP3^{.565} \cdot SIZ^{-.692}.$$
(50B)

Year is similar to 1968:
$$N_M = 0.45N_{M(CALC)}^{.422} \cdot DEF^{.705} \cdot PCP3^{.565} \cdot SIZ^{-.609}.$$
(50C)

Else:
$$N_M = 0.45N_{M(CALC)}^{.422} \cdot DEF^{.705} \cdot PCP3^{.565} \cdot SIZ^{.544}.$$
(50D)

**4.6.3
Relations Specified
by the Results**

4.6.3.1 Density dependence—Projected relations between N_A and the subsequent number of egg masses (N_M) are shown in figures 31-36. Enormous variability occurs in this relation, both from year to year in an area and among areas. In most areas, however, N_A and N_M increased together during each year, as expected. Some likely causes for the variation in this pattern are discussed in section 5.2.2.

4.6.3.2 Parameter stability across budworm density—Continuing a pattern found in previous sections, relations between lnN_M and environmental attributes were sometimes unstable across a range in preceding density.
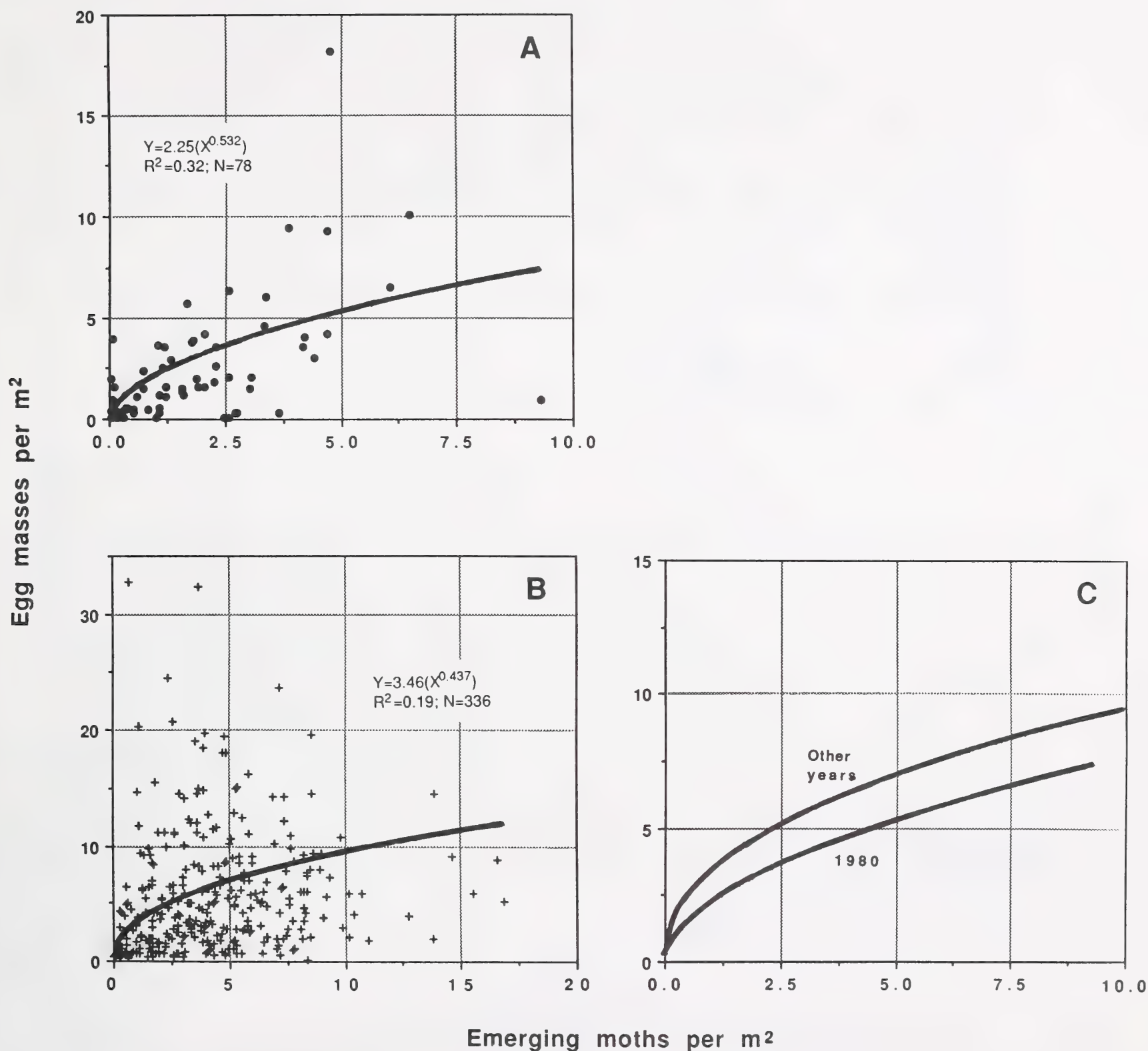
Figure 31—Emerging moths and subsequent egg-mass density in IDA: A, 1980; B, 1981 and 1982; C, comparison, 1980 and 1981-82.

4.6.3.3 Differences across years—Using data from Kirkbride and Wagner (1983), Sheehan and others (1989) described regression equations for calculating potential eggs per female moth. Assuming a mean fresh weight of 98.68 mg per female pupa (derived from I.M. Campbell [1989]), the equations in Sheehan and others (1989) project average values for potential eggs per western budworm female that range from 189.5 on Douglas-fir to 217.7 on Engelmann spruce. These values are very close to values for the eastern budworm that were summarized from several sources (Blais 1953, Greenbank 1956, Jaynes and Speers 1949, Miller 1957) by Miller (1963a). Miller reported that "...estimates of...mean fecundity...when food is ample range from 157 to 209...and
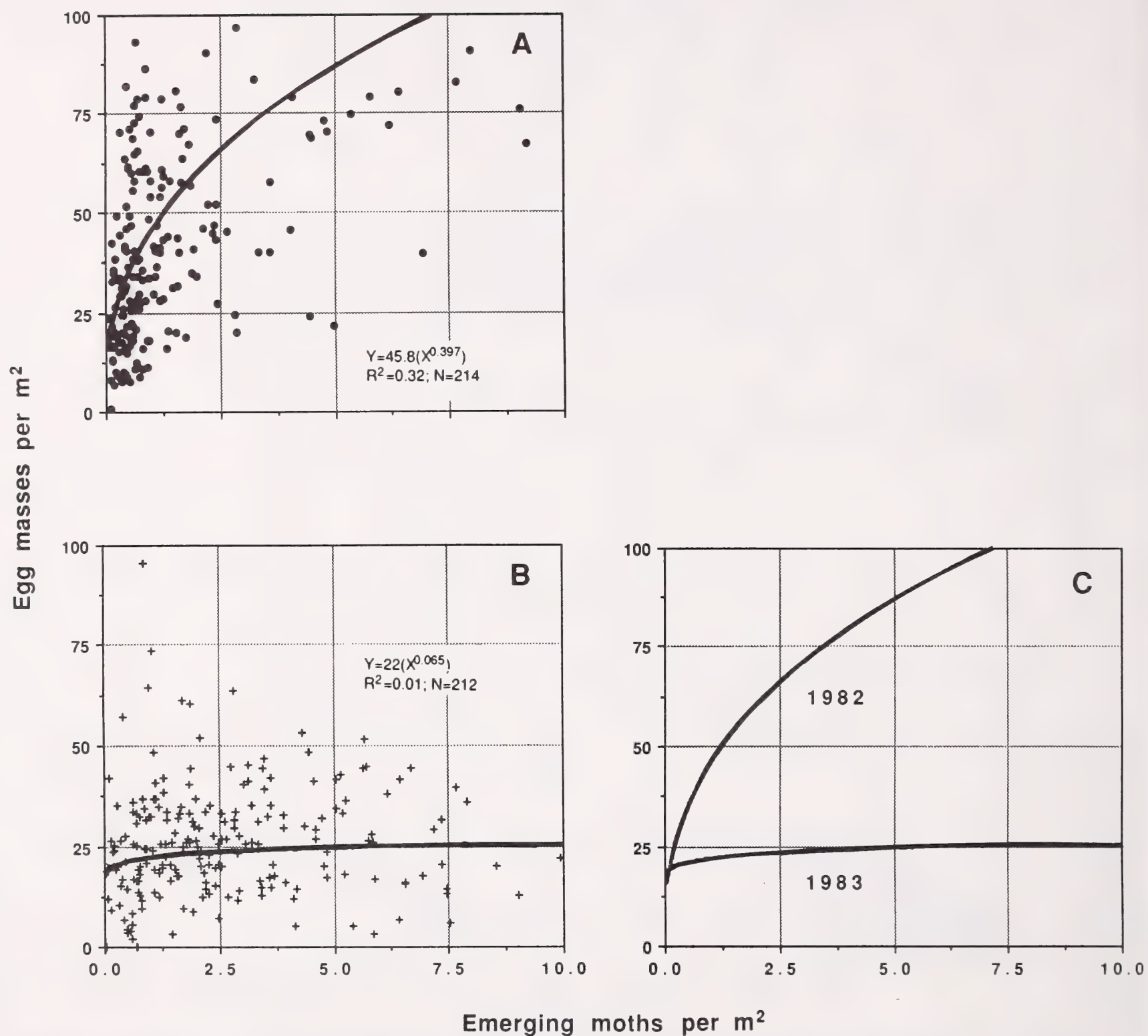
Figure 32—Emerging moths and subsequent egg-mass density in MONT: A, 1982; B, 1983; C, comparison, 1982 and 1983.

support the use of a mean maximum of 200...."

Assuming a mean maximum fecundity of 200 eggs for the western budworm, an adult sex ratio of 1:1 (Campbell and others 1983c), and an average of about 40 eggs per mass (table 3), immigration of gravid moths clearly exceeds the combined effects of emigration and adult mortality when S_A rises above about 2.5 egg masses per emerging moth. Average values of S_A greater than 2.5 were found in every area used in this study during at least one year (figs. 31-36).
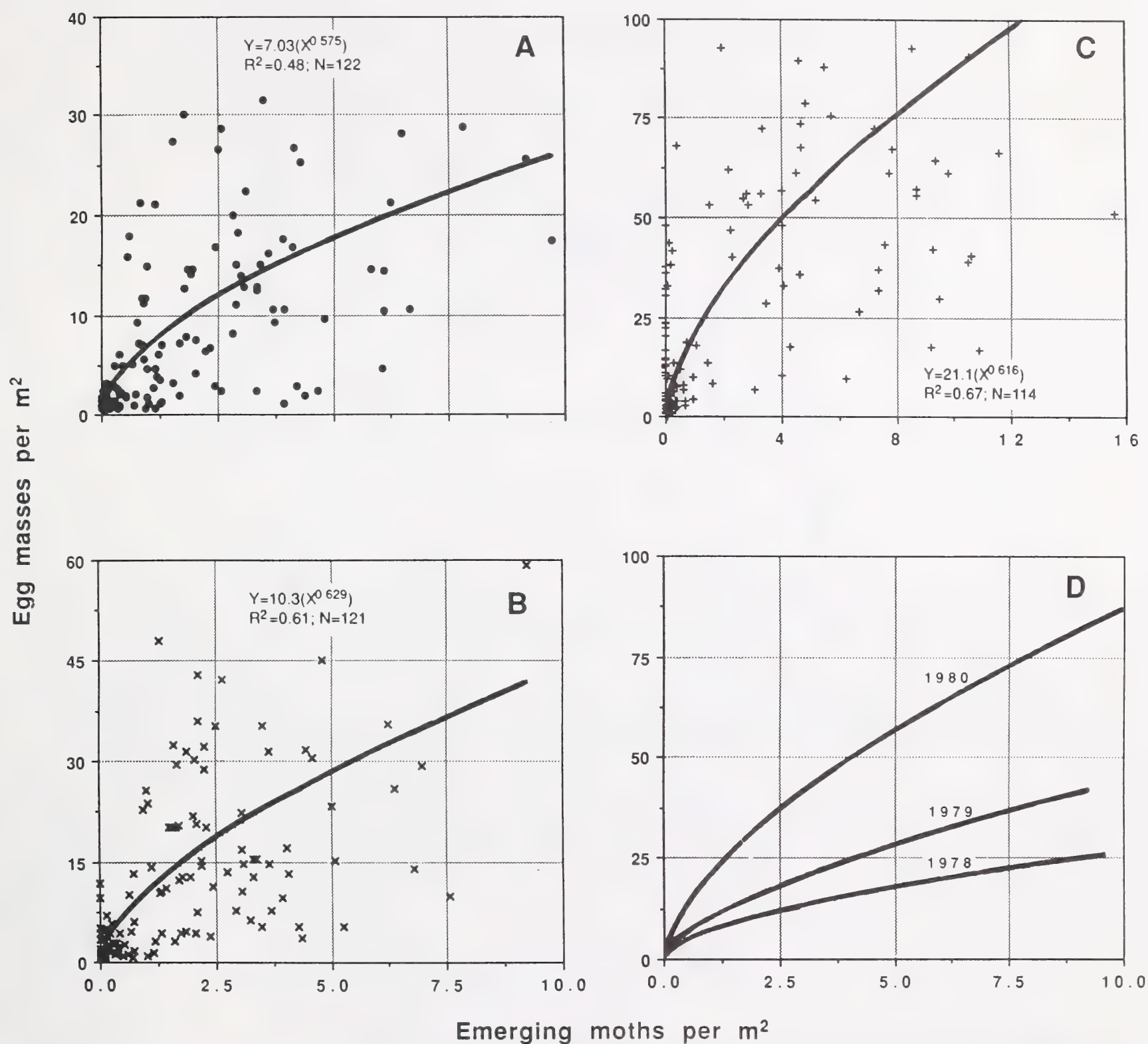
Figure 33—Emerging moths and subsequent egg-mass density in NMEX: A, 1978; B, 1979; C, 1980; D, comparison, 1978, 1979, and 1980.

In New Brunswick, Greenbank and others (1980) used radar to conclusively demonstrate that mass flights of gravid eastern budworm females are rather commonplace. In contrast, long-range moth dispersal has rarely been observed in the western budworm (Carlson and others 1985a, Carolin 1987), and some mass flights may even have been reported as UFOs, or unidentified flying objects (Callahan and Mankin 1978). Brodeur and others (1987), however, show conclusively that mass flights also occur in the western species. These authors report that waterborne patches of western budworm moths on the northeastern Pacific Ocean were
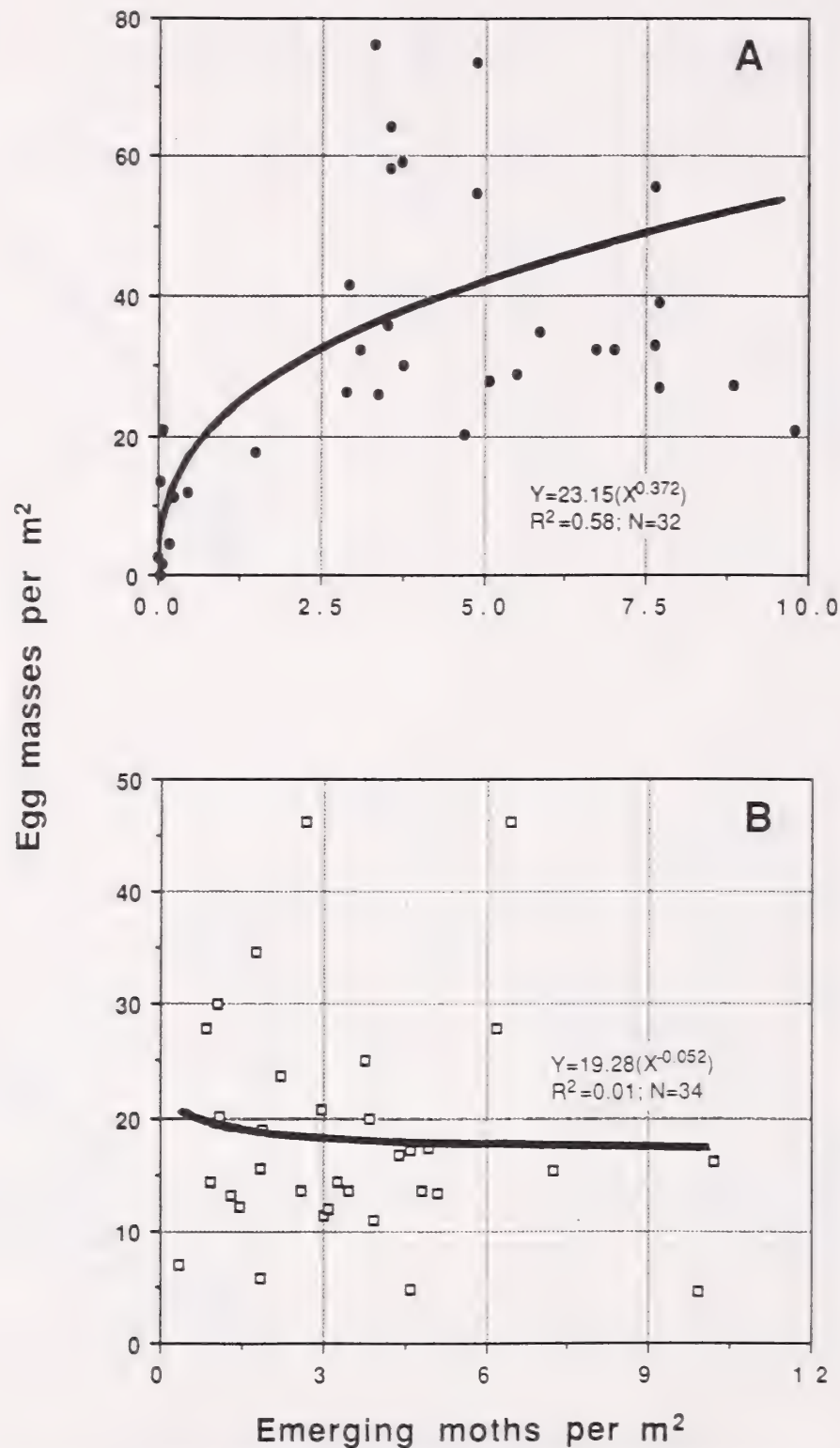
Figure 34—Emerging moths and subsequent egg-mass density in DAMAG:
A, 1979-80; B, 1981-83.

...abundant and large enough to be highly visible from the deck of a ship...at several stations off Wecoma Beach, Oregon, on 25 July [1984].... [This insect was] by far the dominant prey item by weight in the coho [salmon, *Oncorhynchus kisutch* (Walbaum)] stomachs at the same stations where this [prey] species occurred in the neuston [surface]....several juvenile coho...had stomachs that were distended with over 100 of these insects...

During this time, floating patches of western budworm adults were visible off the Oregon coast for up to 29 nautical miles (52.7 km) offshore (Pearcy 1992). The weather pattern thought to be responsible for this dramatic westerly budworm movement is described in
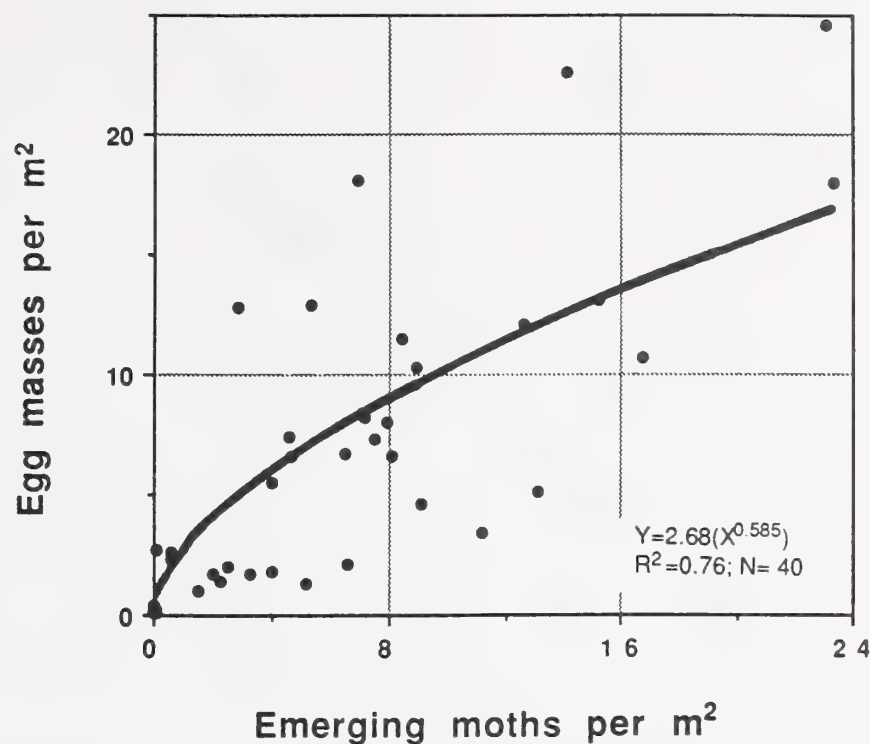
Figure 35—Emerging moths and subsequent egg-mass density in COLO and PNW.

Brodeur and others (1987). As expected, similar large floating patches of eastern budworm adults have also been reported off eastern North America (Cheng and Birch 1978).

The above results greatly support and extend prior conclusions that redistribution of eggs by adult moths is a major factor in the population dynamics of the western budworm (Campbell 1987, Campbell and others 1983a). The implications of these findings are central to much of the discussion in Chapter 5.

4.6.3.4 Influence of recent insecticide treatment—In NMEX, the equations project lower values of S_A in plots that had been treated (fig. 37). The inverse relation between insecticide treatment in one year and S_A in subsequent years supports my earlier suggestion (sections 4.2.2.1 and 4.2.2.4) that moths may be attracted to plots that are somewhat more defoliated. Also, mean egg-mass density in both treated and control blocks in NMEX for 1977 through 1983 is summarized in figure 38. As shown earlier for defoliation (fig. 24), these results show that lower egg-mass densities were found in treated blocks for six posttreatment years.

4.6.3.5 Influence of on-site defoliation—Egg-mass density and percent defoliation of current-year foliage increased together in WXBASE (equation 50), which suggests that fecund moths gravitate to stands that exhibit some recent defoliation. These results may also extend the biological rationale for observations by others (Cates and others 1983, Redak and Cates 1984) that adjacent host trees of the same species sometimes vary considerably in defoliation. In addition, they are compatible with the preliminary finding by McDonald (1985) that heritable characteristics of the host tree may affect ovipositional preference by the western budworm.

4.6.3.6 Interstand influences—In IDA, S_A was closely related to both $DST_{(n)}$ (the distance from the plot to the current edge of visible defoliation) (table 24), and SIZ (the proportion of a 20 000-ha area around the plot that was visibly defoliated during the
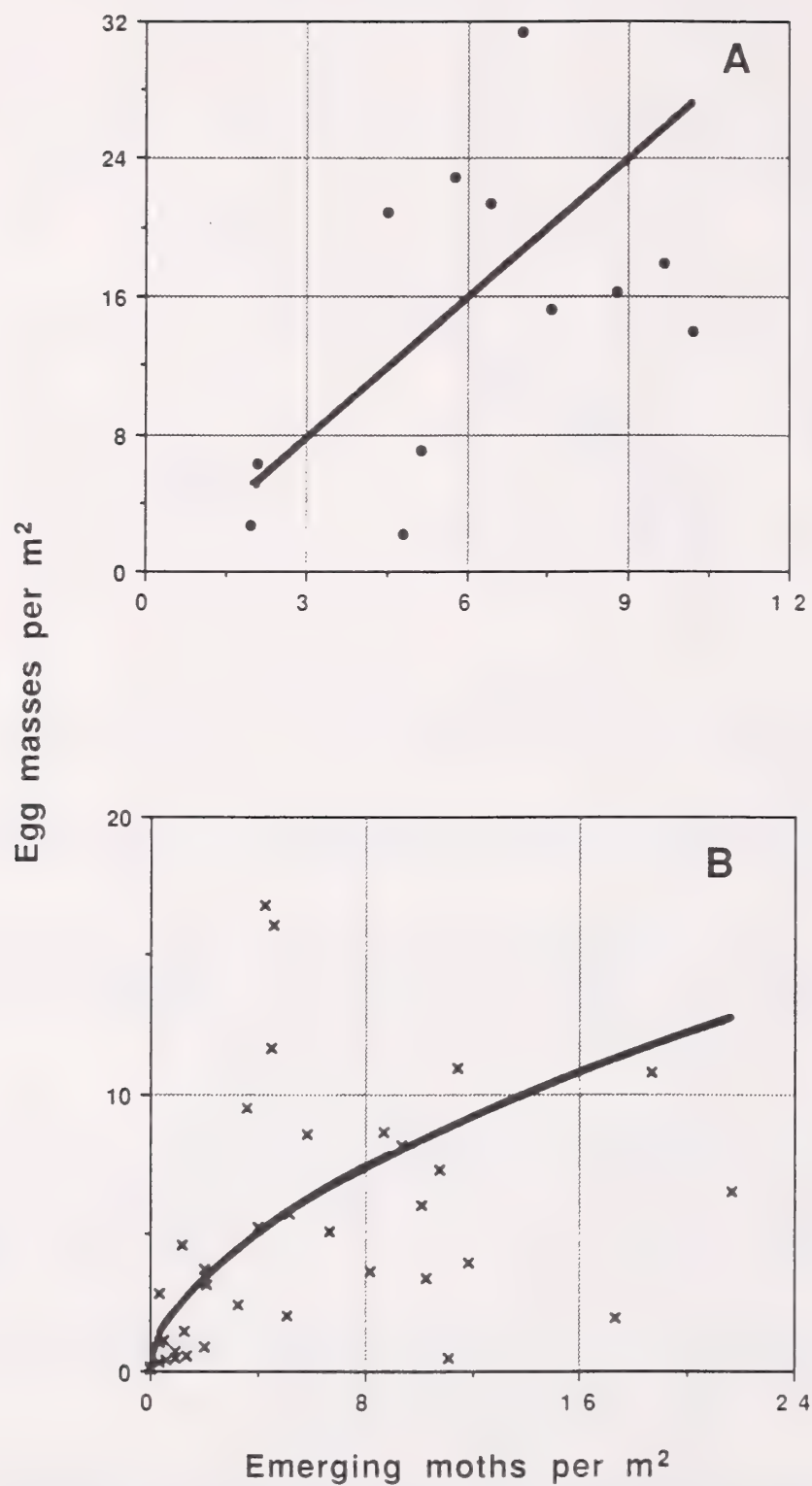
Figure 36—Emerging moths and subsequent egg-mass density in OREG:
A, 1985 and 1986; B, 1984, 1987, and 1988.

season the egg masses were deposited) (table 24). The area selected for IDA is characterized by more-or-less continuous forest for many miles in all directions. In this area, the relation found between SIZ and subsequent N_M undoubtedly results in part from short-range dispersal flights by gravid moths. As a consequence of such flights, more egg masses per emerging moth would necessarily be deposited in plots near dense populations.

Patterns of egg-mass deposition were also related to SIZ in WXBASE [equation (50)]. Here, the relation was not consistent from year to year. SIZ and N_M increased together

Plot A: $Y=5.64(X^{0.303})$ $R^2=0.14; N=85$

Plot B: $Y=12.8(X^{0.608})$ $R^2=0.42; N=272$

Plot C: Control plots / Treated plots

Y-axis (A and B): Egg masses per m²
X-axis: Emerging moths per m²
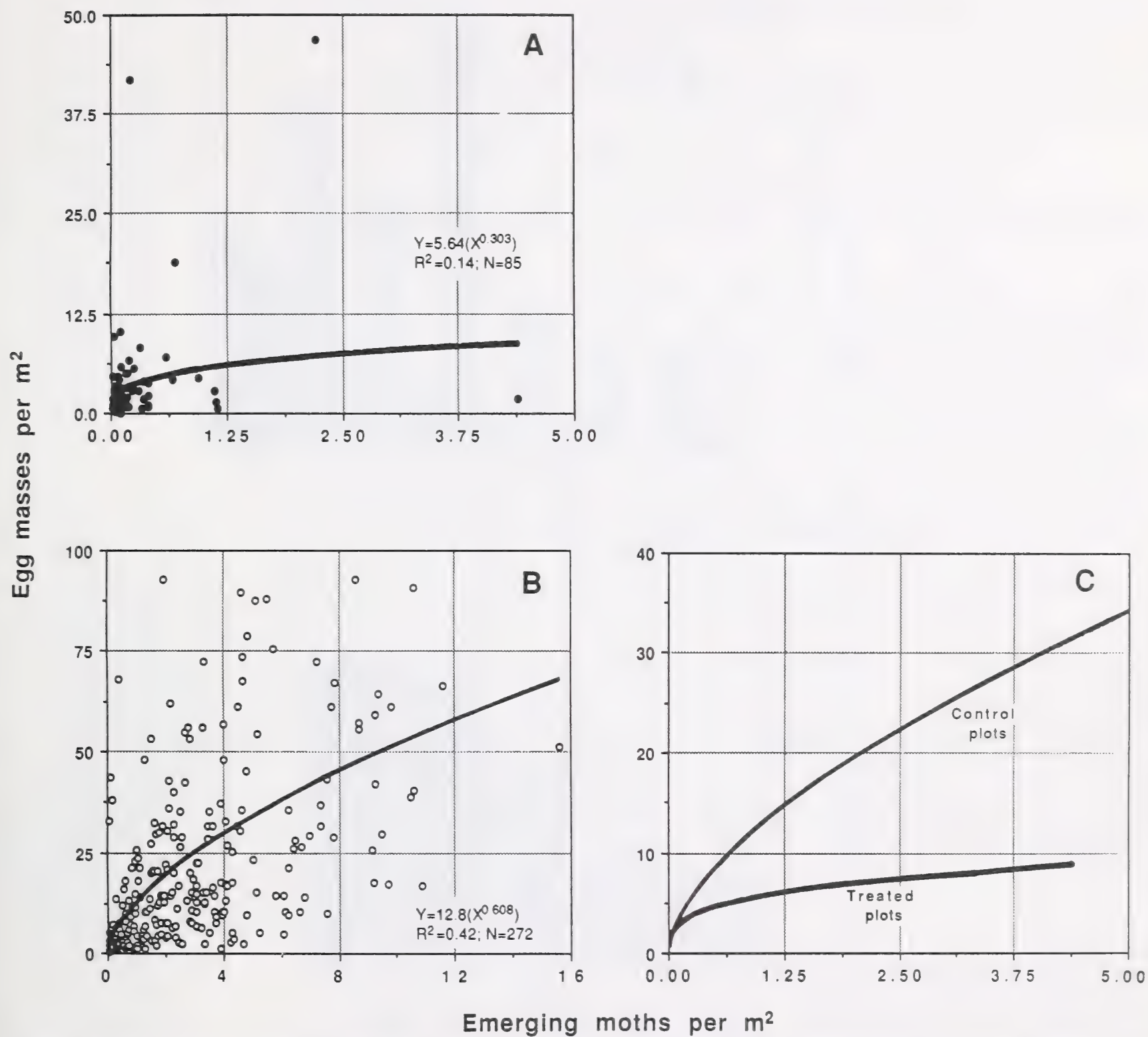
Figure 37—Insecticide treatment and the relation between emerging moths and egg-mass density during subsequent years in NMEX: A, treated plots; B, control plots; C, comparison, treated and control plots.

during most years in the decade between 1960 and 1969, but during 1963, 1965, and 1968, they were inversely correlated.

Processes that may be responsible for the apparent "pulsing" in the relation between SIZ and N_M are discussed in section 5.2.2 and 5.2.3.

4.6.3.7 Influence of site—In IDA, S_A and elevation increased together. In MONT, S_A was highest among the plots that were at and slightly above the mid-range in the elevational
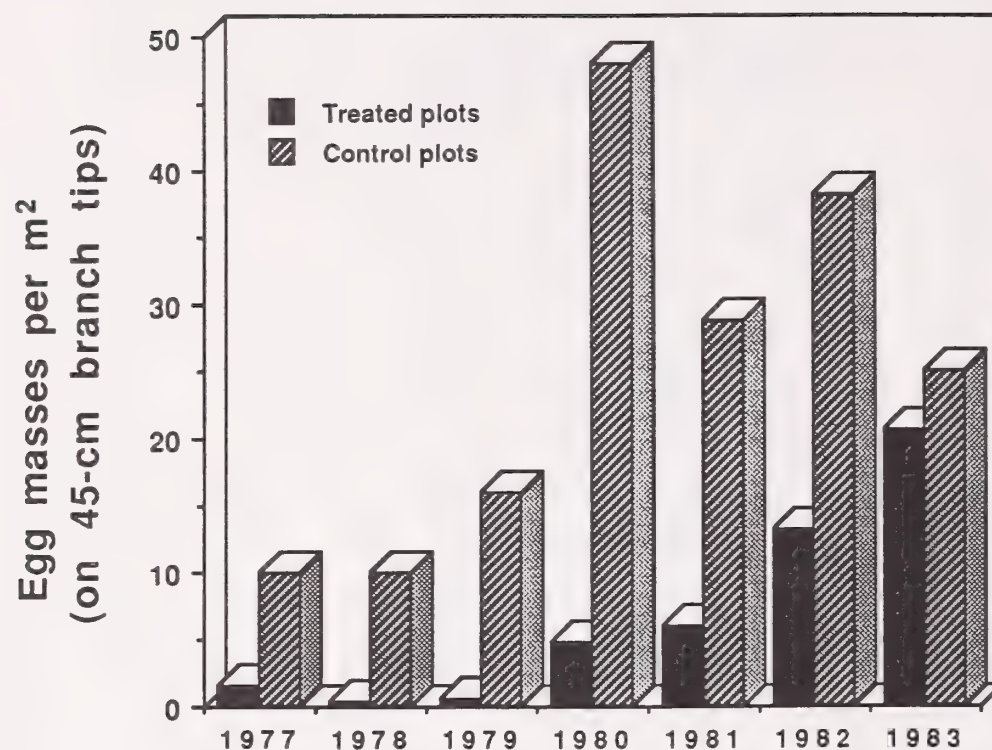
Figure 38—Egg-mass densities in treated and control plots in NMEX from 1977 (treatment year) to 1983 (from Telfer 1984).
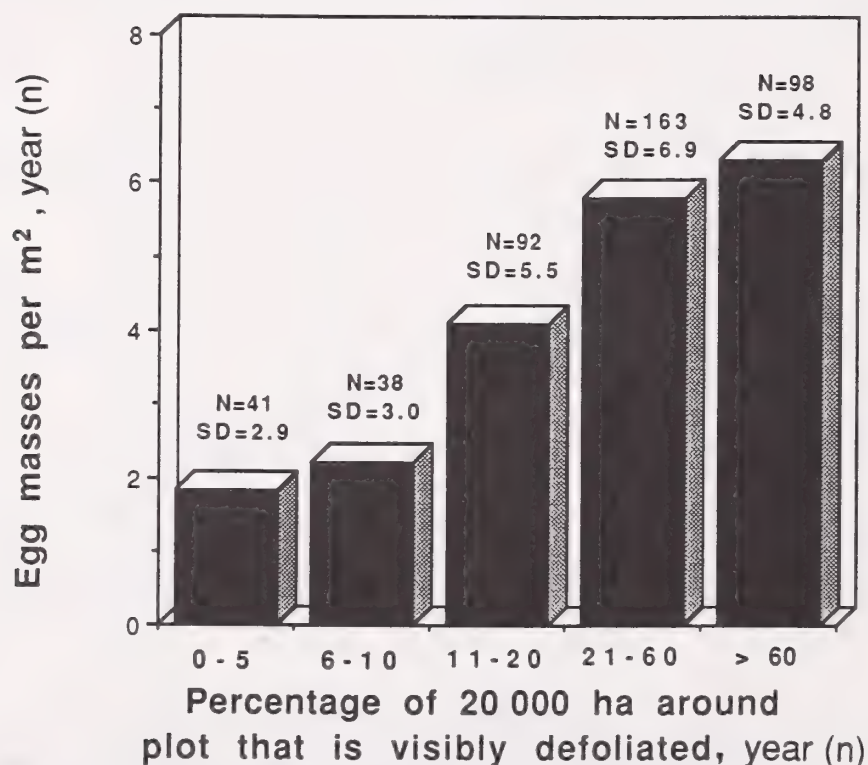
Figure 39—Outbreak size and egg-mass density in IDA.

gradient. And in NMEX, S_A was lowest in the top 20 percent of the elevational gradient. Together, those relations reflect an apparent tendency for fecund moths to aggregate near the elevational center of their host stands. This pattern provides a further explanation for findings by others (Heller and Kessler 1985, Marsden and others 1986, Shepherd 1985) that defoliation tends to be greatest across an elevational midrange of the hosts.

In IDA, a strong inverse relation was found between S_A and site wetness. Mean values of S_A as related to site wetness in IDA are:

Plot category	Number of plot-years	Mean S_A	Standard error
Wet sites	100	1.72	0.24
Other	314	2.97	.41

This relation probably reflects the inverse relation between S_L and site wetness that was noted earlier (section 4.5.3.3).

Average S_A in NMEX was higher on sites classified as having inherently low productivity, at least at moderate to high densities. Unfortunately, the index of inherent productivity I used is based on a subjective appraisal that included observers' impressions of the physical and vegetative aspects on that site. During a prolonged outbreak, the appearance of the stand is a function, in part, of past budworm activity. Also, interior Douglas-fir is the potential climax species in the northern Rocky Mountains on sites that are too droughty for either the true firs or Engelmann spruce. And in the central and southern Rockies, Douglas-fir is more adaptable than white fir (Wellner 1978a). Thus, cause and effect relations between this index, prior budworm activity, and the ecological requirements of the various host species are scrambled. Nevertheless, both these results and results presented earlier (tables 20, 23) support Stoszek and Mika's (1985) recommendation for silvicultural treatments that can improve rates of nutrient cycling and availability of moisture and nutrients as ways to reduce the effects of budworm outbreaks.

4.6.3.8 Influence of stand—As previously noted, observed S_A was commonly greater than the inherent capacity of the emerging moths to lay eggs. Thus, the positive relations between S_A and the proportion of Douglas-fir in the overstory (tables 24-25, figure 40) in IDA, MONT, and NMEX along with the negative relation in IDA and NMEX between S_A and the proportion of true fir and spruce (tables 24, 26, figs. 41 and 42) leave no doubt that western budworm adults gravitate to stands with a high proportion of Douglas-fir. In part, at least, these results both confirm and extend those of Schmid and Farrar (1982). They also provide a simple rationale for findings by others that defoliation is correlated with the proportion of host species in the stand (Fauss and Pierce 1969, Heller and Kessler 1985, Stoszek and Mika 1985).

The above results do not support suggestions of Schmidt and others (1983) and Carlson and others (1985a) that the tendency of the true firs to undergo extensive budworm defoliation (section 4.4.3.7) reflects a higher budworm "feeding preference" for these hosts. Undoubtedly, however, they do reflect findings by several investigators (Beckwith, personal communication; Blake and Wagner, personal communication) that the efficacy of foliage conversion (weight gain of the budworm per weight of foliage consumed) is much higher for larvae fed on Douglas-fir. Using these unpublished data, Sheehan and others (1989) derived efficacy of conversion indices for Douglas-fir that are about 1.5 times as high as the indices for grand fir and white fir. Interestingly, this same ratio (1.5) would be projected from the NMEX data (fig. 26), assuming equal budworm densities on both hosts and about 50 percent defoliation on the Douglas-fir. Like the previously discussed finding that western budworm moths gravitate to Douglas-fir, the high efficacy of conversion index for Douglas-fir foliage emphasizes the inherently close host-pest linkages between these two species.
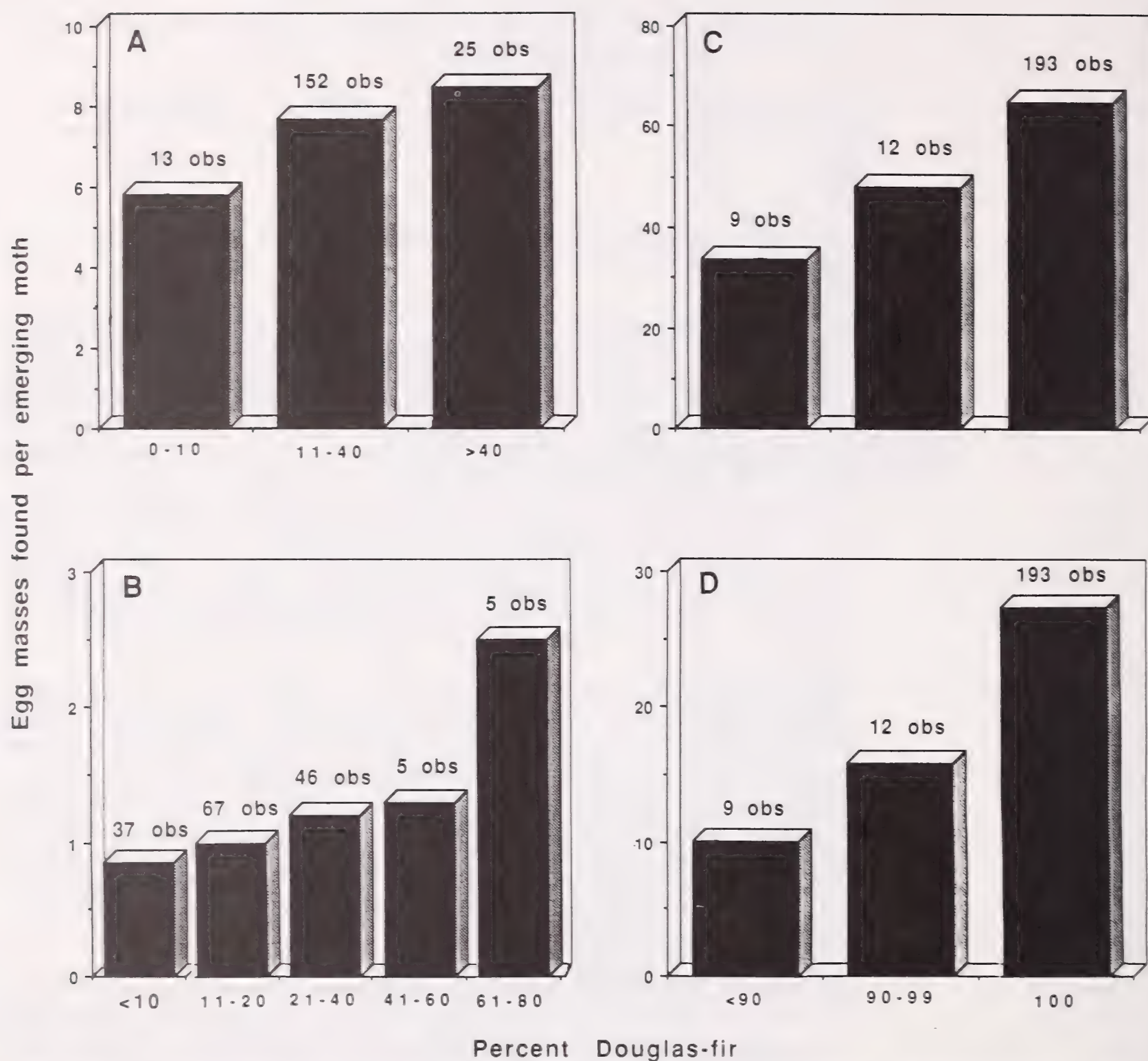
Figure 40—Proportion of Douglas-fir in the overstory and the number of egg masses deposited per emerging moth: A, NMEX; B, IDA; C, MONT in 1982; D, MONT in 1983.

In MONT, an inverse relation was found between S_A and stand age. Mean values of S_A related to stand age in MONT are shown below:

Plot category	Number of plot-years	Mean S_A	Standard error
≤ 50 years	136	52.7	5.0
51-75	164	47.7	4.7
76-150	100	29.9	4.6
> 150	28	36.8	12.2
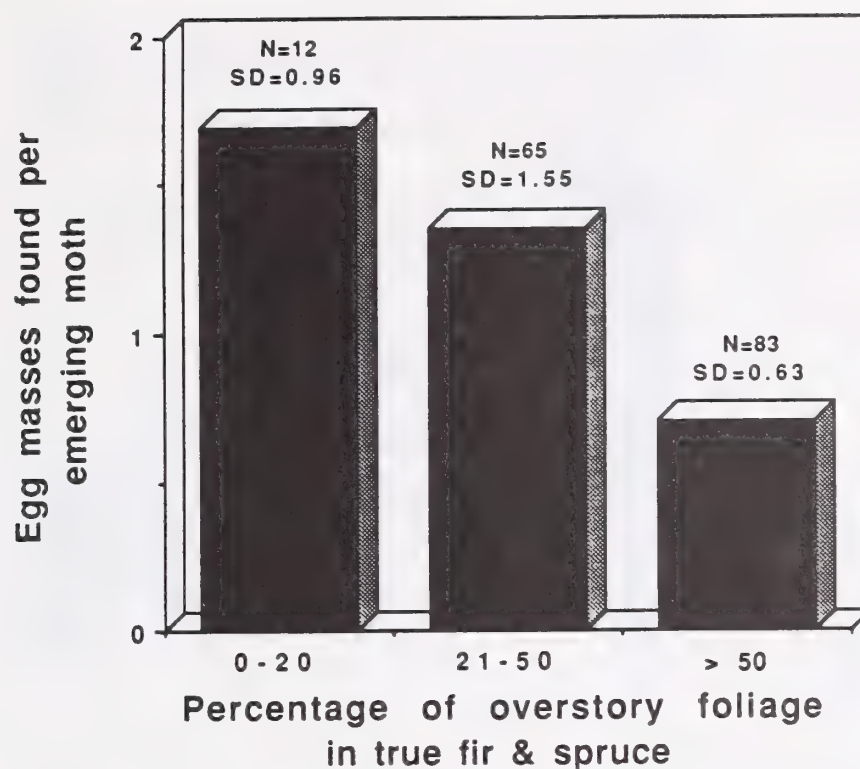
Figure 41—Proportion of true fir and spruce in the overstory and the number of egg masses deposited per emerging moth in IDA; four or more emerging moths per m².

These surprising results suggest that old-growth Douglas-fir is less attractive to migrating moths than somewhat younger stands. Because similar relations between host age and S_A were not found in any other area, speculating on possible causes for this apparent relation in MONT would be premature.

4.6.3.9 Influence of weather—In WXBASE, mean trend in egg-mass density was highest (about 5 percent higher) during years when total precipitation during May, June, and July was between 10.5 and 14 cm. These results are discussed in section 5.2.6.2.

4.7 Some Comparisons Among Three Budworm Species

Both the eastern and the western budworms are capable of colonizing the other's hosts (Eidt and MacGillivray 1972, Harvey 1983). Powell (1980) concluded "...names applied to... [various] *Choristoneura*, particularly in western North America, are little more than signs posted...on mosaics of differing populations." Although limited trials with adult moths have demonstrated some sexual isolation between the two species (I.M. Campbell 1967), Volney (1985) assumes that they would "doubtless" hybridize in nature. Volney bases this assumption on studies of sympatric populations of the western budworm and the Modoc budworm, *C. retiniana* (Walsingham), in south-central Oregon (Liebhold and others 1984, Volney and others 1984). Volney suggested that gene flow between the western and eastern budworms "...would be adequately described by a riparian model with a western source at high elevation, in which colonists are driven east/northeast by the prevailing circulation patterns." Although Harvey (1985) noted that "the western and northwestern limits of the eastern budworm are not well documented," he concluded that *C. fumiferana* and *C. occidentalis* "...are well separated geographically...are probably not sympatric anywhere and...are widely recognized as good species."

Unlike the broad host acceptability among the budworm group associated with spruces, Douglas-fir, and true firs, the separation between this group and the budworms associated with pines is "...virtually complete; rarely does complete development occur on a
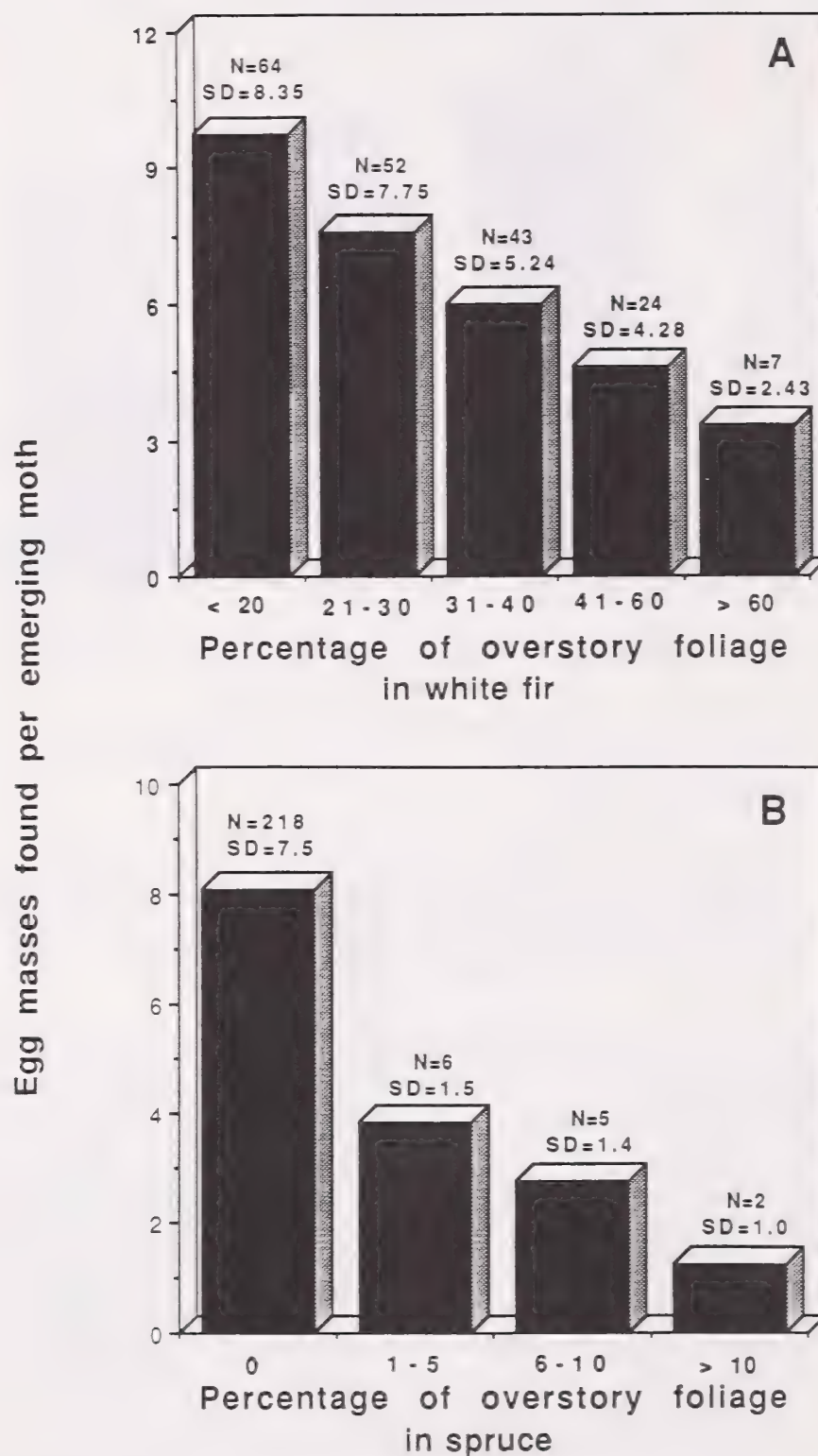
Figure 42—Overstory composition and the number of egg masses deposited per emerging moth in NMEX: A, white fir; B, Engelmann spruce; one or more emerging moths per m².

host of the other group" (Harvey 1985). Nevertheless, all crosses attempted among the conifer-eating *Choristoneura* species have produced viable offspring that have survived to become adults, and Harvey (1985) reported that "...the existing evidence indicates no mechanical or gametic isolation among members of...[a] group...." that includes both the eastern and western budworms and the jack pine budworm.

Because of the many apparent similarities between the population dynamics of the western and eastern budworm and the jack pine budworm, this section compares a few age-

interval survival rates of the three species. Subsequently (section 5.2.8.5), I also use some of this same information to critique Royama's (1984) rationale for rejecting Morris's (1963d) dual-equilibrium theory for the eastern budworm.

4.7.1
Eggs to
Emerging Moths

Survival rates from eggs to emerging moths (S_G) are shown across an outbreak of the western budworm in eastern Oregon (fig. 43A), the eastern budworm in western New Brunswick (fig. 43B), and the jack pine budworm in Michigan (fig. 43C). For the eastern budworm, the points represent generation survival in a single plot (plot G4), but for the western and jack pine budworms, they represent mean values for all the plot-years in OREG and the Michigan populations described in Foltz (1969), respectively. Because the author of figure 43B noted that "...the rise and fall of population density in...[plot G4] followed much the same pattern as...other areas...." (Royama 1984), and because he repeatedly used the numerical trend in this plot as an example (Royama 1981, 1984), I assume that this trend represents typical numerical behavior for the eastern budworm during an outbreak. As the outbreak progressed, S_G systematically declined in both the eastern and western species. Similarly, S_G also declined in the jack pine budworm during the three years for which life table data are available on this species in Michigan.

4.7.2
Eggs to Half-Grown
Larvae

Figure 44 shows survival from eggs to half-grown larvae (S_s) in the eastern budworm as a function of egg density. The relation was derived from an outbreak in western New Brunswick using information in Mott (1963a). Equivalent survival rates in the western and jack pine budworms for this interval are shown on a logarithmic scale in figure 45. To develop the relations shown in figure 45B, I deleted an outlier observation from the data subset for 1968. In that particular plot-year S_s was only 0.012, even though starting egg density was only about 38 eggs per 100 shoots.

On an arithmetic scale, early survival in all three budworm species is shown in figure 46 as a function of egg density. In the eastern budworm, S_s and N_E were only related at densities below about 100 eggs per m^2. Clearly, the drastic reductions in S_s during prolonged outbreaks of the western budworm, such as those shown in figure 46 for MONT and NMEX, were not found in this population of the eastern budworm. Apparently, the life system of the eastern budworm does not include the property that systematically depresses S_s in the western species during extended outbreaks. As Royama (1984) noted: "...only in [one plot] did [early instar survival in eastern budworm] show an apparently decreasing trend [across the course of the outbreak]." Interestingly, S_s in the jack pine budworm shows both a density-dependent pattern and systematic year-to-year differences similar to those found in the western budworm. I return to this subject in section 5.2.3.

4.7.3
Half-Grown Larvae
to Emerging Moths

4.7.3.1 Outbreaks—Figure 47 shows eastern budworm survival from third instar to pupae as a function of third-instar density. In populations of both eastern and western budworms, systematic reductions have been noted across the course of an outbreak in survival rates from half-grown larvae to emerging moths (Royama 1984, section 4.5.3.2). Figure 48A, however, which compares this latter rate during an eastern budworm outbreak with one by the western budworm, only shows year-to-year changes in populations of the western budworm. For the latter species, the relation shown represents the OREG outbreak [equation (45)]. For the eastern budworm, the relation is derived primarily from Watt (1963), with the survival rate of late pupae set at 0.656 (Morris 1963a). In populations of jack pine budworm, survival during this interval was related to larval density only during 1967, just one of the three years for which data are available. This relation is shown in figure 48B.
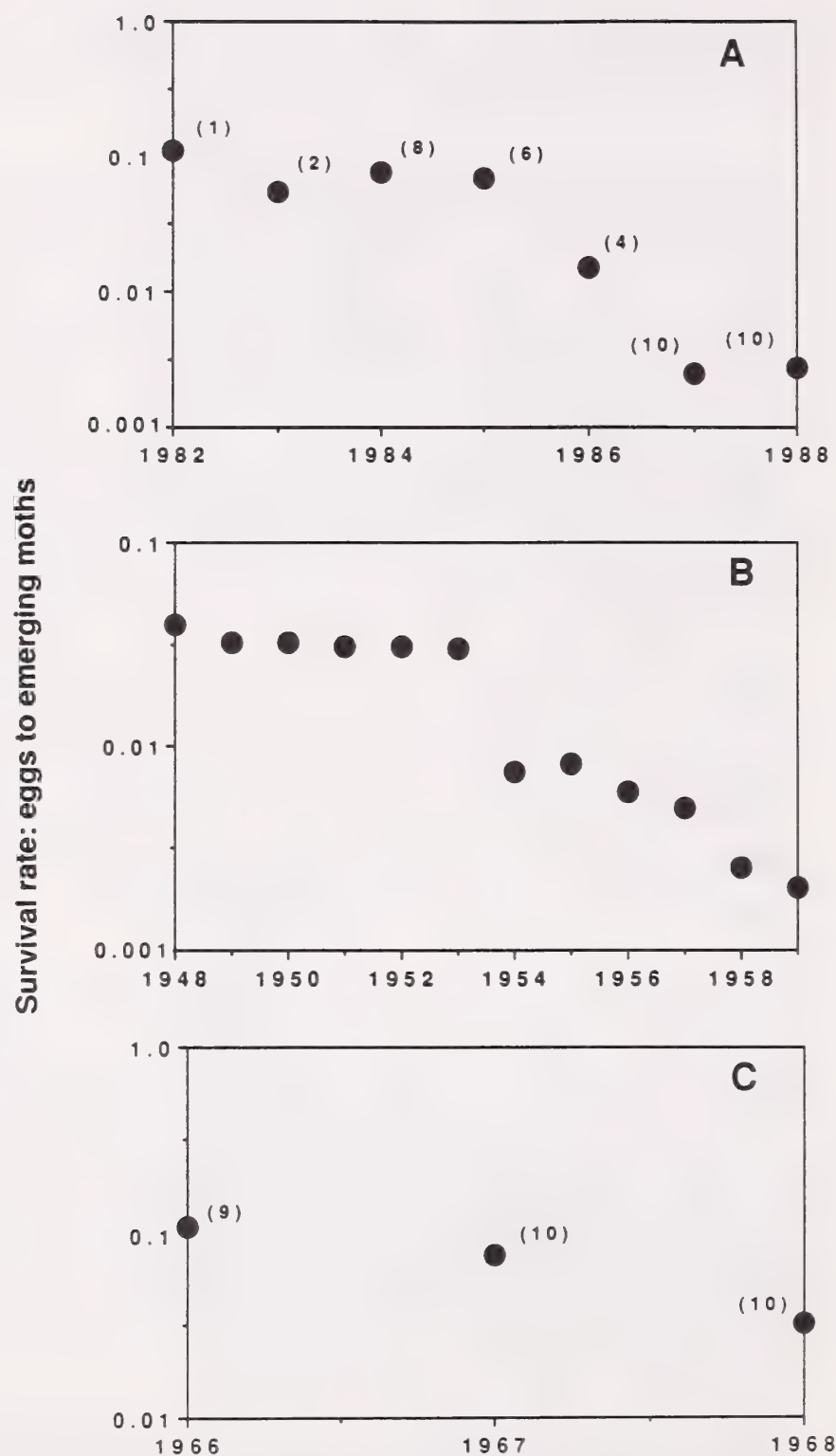
Figure 43—Survival rates from eggs to adults across the course of an outbreak: A, western budworm in OREG; B, eastern budworm in western New Brunswick (after Royama 1984); C, jack pine budworm in Michigan (data from Foltz 1969); number of plots are shown in parentheses.

As Royama (1984) pointed out, Watt (1963) pooled data from many plots and several years to develop his equation. Because of this pooling, Royama suggests that the relation Watt derived between N_L and subsequent survival may be somewhat misleading. Nevertheless, at least three comparisons between the survival trajectories for the three species seem valid. First, in populations of the eastern budworm, average survival continued to increase well beyond densities where survival was already declining rapidly in the western budworm. Second, across densities from about 1 to 20 half-grown larvae per m², survival
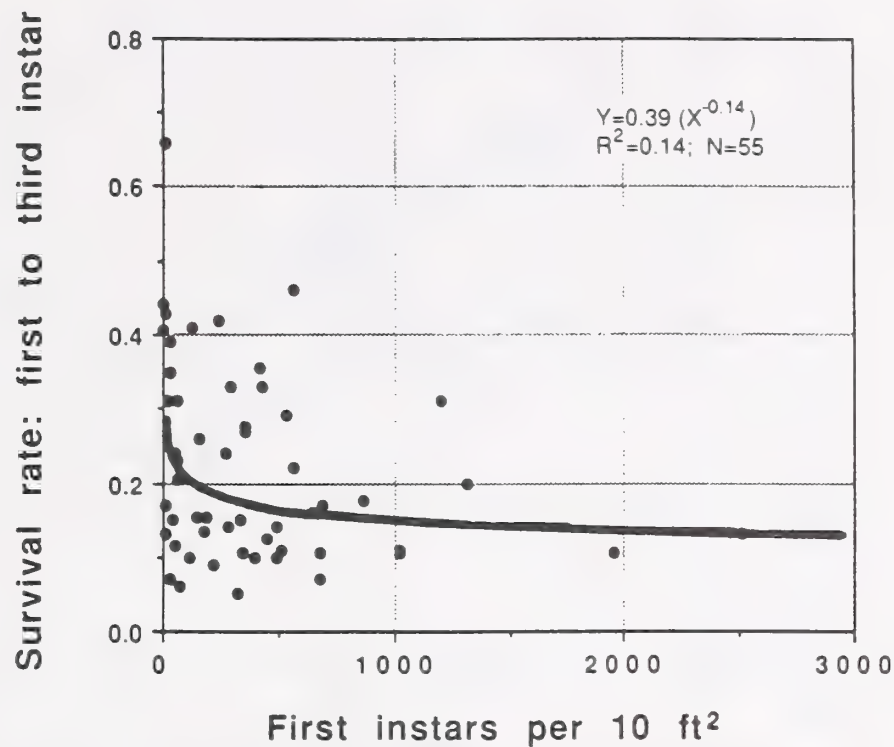
Figure 44—First-instar density and survival rate from first instar to third instar in eastern budworm (adapted from Mott 1963a).

in eastern budworm is remarkably similar to that found in western budworm during a recent phase (1986-88) of the OREG outbreak. Third, survival in the jack pine budworm during 1967 follows a similar inversely density-dependent pattern to those found in both the eastern and western budworms across a midrange of larval densities.

Working almost exclusively from graphic comparisons, Royama (1984) concluded that the declining trend in S_G of eastern budworm across an outbreak results from a decline in survival among late instars. In seeking the cause of this decline, Royama found a close relation between total mortality among large larvae and a variable representing total mortality from parasites, disease, and "unknown," as determined by laboratory rearing (Neilson 1963). Royama named the sum of mortality from disease and unknown "the fifth agent." Commonly, this mortality exceeded 50 percent in laboratory rearings of field-collected larvae.

Blais (1985) found no apparent increase in mortality resulting from "undetermined factors" during the decline phase of the 1947-58 outbreak in Quebec—an outbreak that was both contemporaneous with and adjacent to the one investigated by Neilson (1963). Raske (1985), however, reported mortalities similar to those found by Neilson among laboratory rearings of larvae collected from collapsing populations in Newfoundland. Among these insects, the proportion dying of unknown causes "...tended to be low during early June (10 to 20 percent), rose sharply during late June (up to 90 percent) and dropped to very low levels (0 to 10 percent) during late pupal collections." Raske noted that "parasites were not the cause [of this mortality], or [was] any known or recognizable disease...."

To my knowledge, rearings of field-collected western budworm have rarely yielded mortality rates from these categories that are anywhere near as high as those found by Neilson and Raske. In populations of western budworm, the evidence suggests that systematic declines in survival across an outbreak are somehow linked to defensive reactions by the host trees, for reasons discussed in sections 5.2.3 and 5.2.5. Interestingly, such reactions were not explicitly considered in Royama's 1984 monograph.
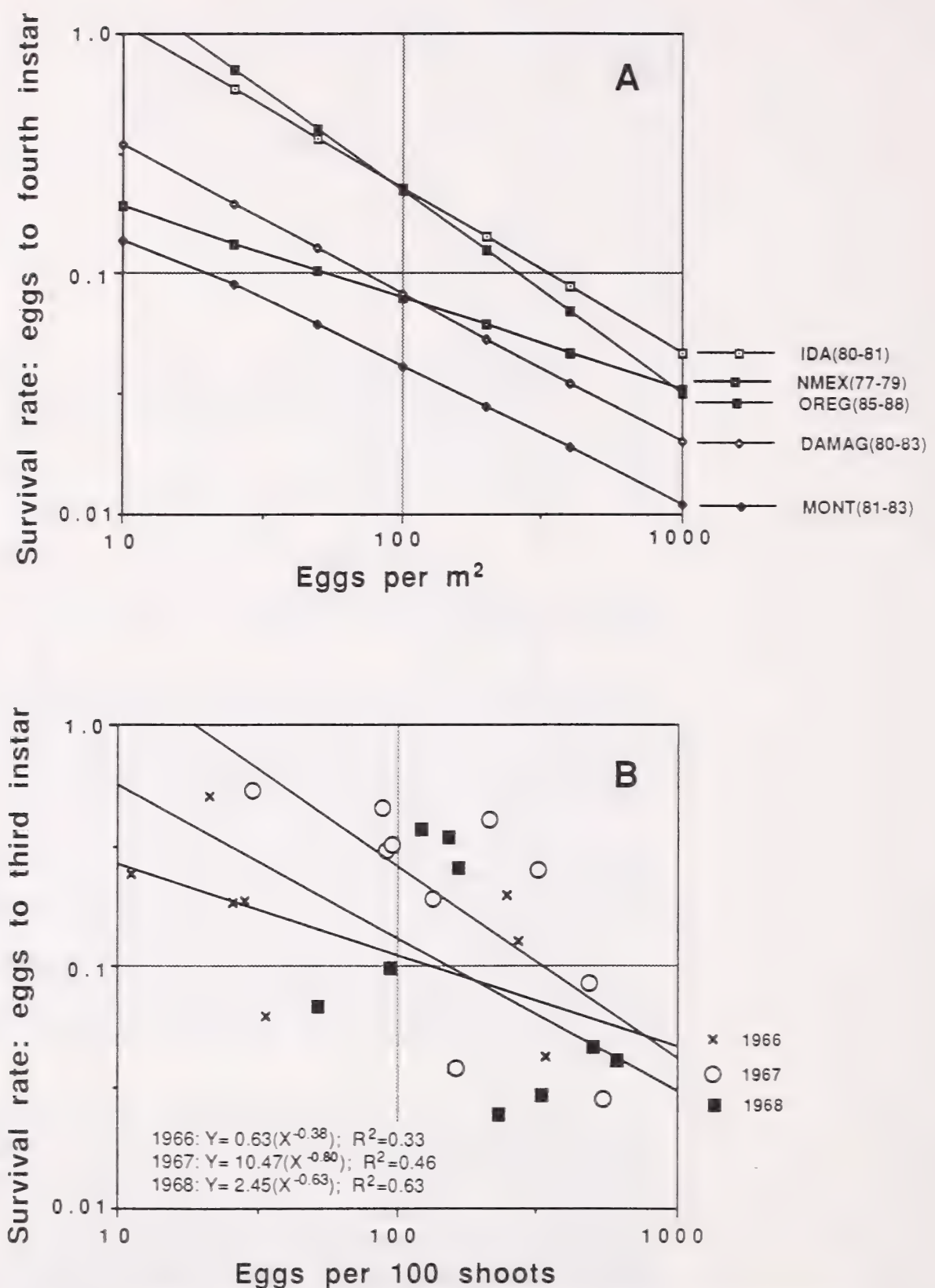
Figure 45—Survival rates from eggs to half-grown larvae (logarithmic scale): A, western budworm (outbreak data only); B, jack pine budworm (data from Foltz 1969).

For all three budworm species, the processes that appear most likely to be responsible for increasing values of S_L across a midrange of larval densities are discussed in section 5.2.1.3.

4.7.3.2 Sparse conditions—Several investigators have shown that populations of eastern budworm sometimes persist for extended periods at or below one fourth instar per m² of foliage. Royama (1984), for example, shows that the population in plot G4 (New
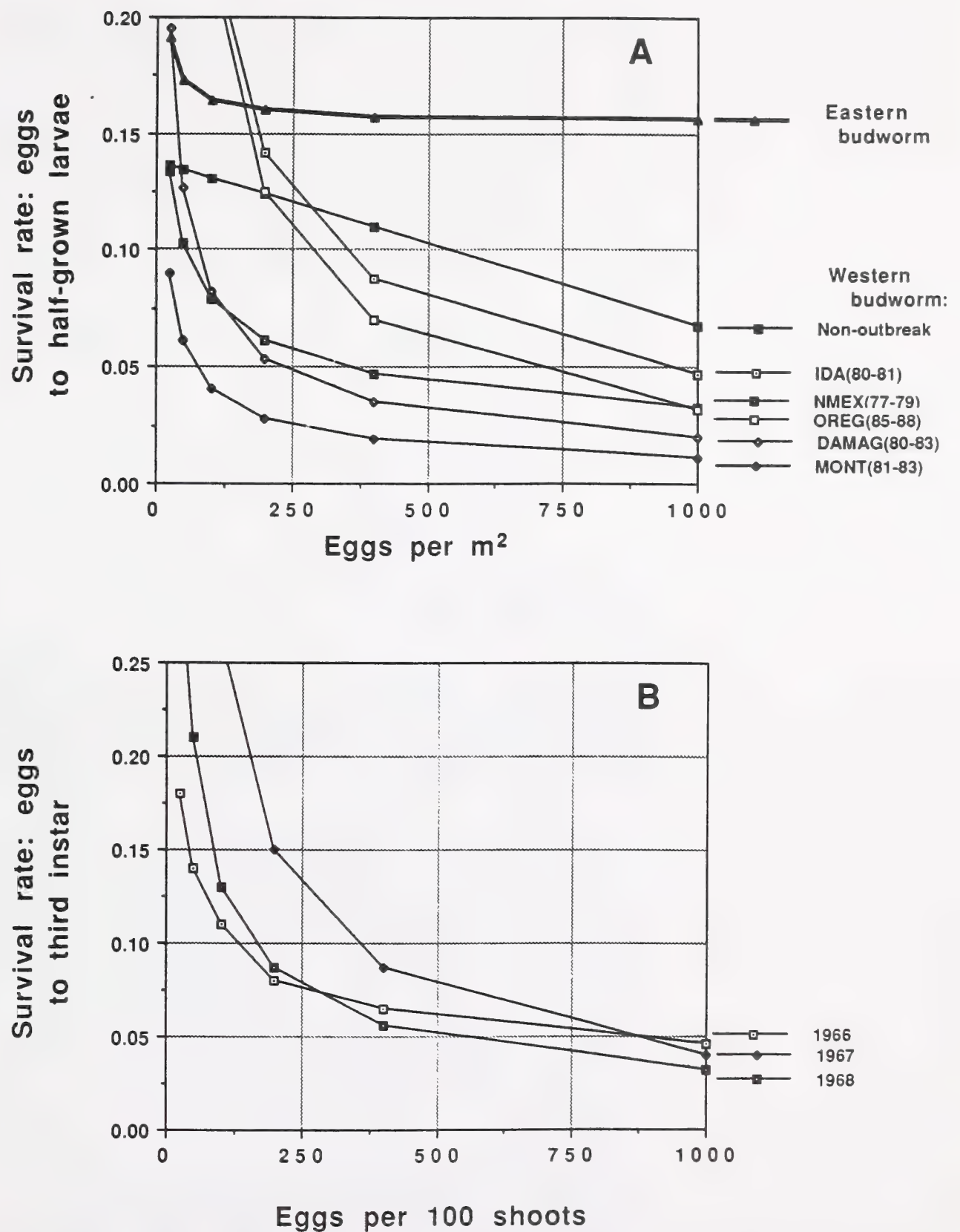
Figure 46—Egg density and projected survival to fourth instar (if western budworm) or third instar (if eastern budworm or jack pine budworm). A, eastern and western budworm (eastern budworm relation adapted from Mott 1963a); B, jack pine budworm (data from Foltz 1969). For eastern budworm, egg survival is assumed to be 0.812 (Morris 1963a).

Brunswick) remained in a density range between about 0.05 and 1 larva per m² for 10 consecutive years (1959-68). Also in northwestern New Brunswick, Miller and Renault (1981) estimated third-instar density in one stand of young balsam fir at 0.076, 0.026, and 0.021 larvae per midcrown branch in 1961, 1962, and 1963. And in the Adirondack Mountains of northern New York, we found a total of 27 nominal fourth instars on 4,537
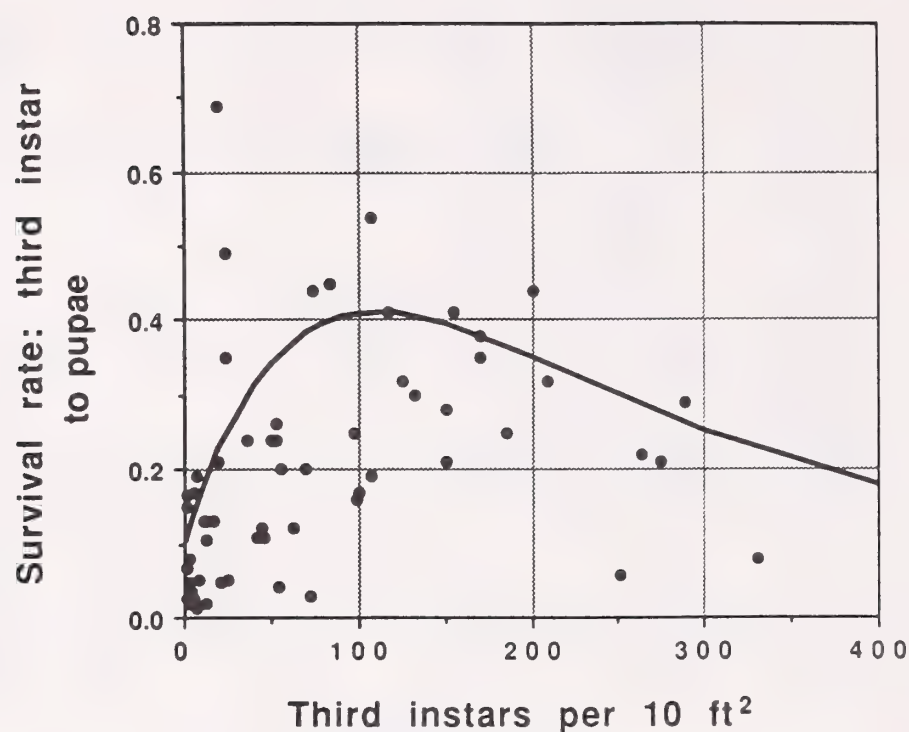
Figure 47—Third-instar density and survival rate to pupae in eastern budworm (adapted from Watt 1963).

45-cm branch tips drawn from all portions of host trees about 4 m tall. In the latter study, average fourth-instar density in four plots was estimated at 0, 0, 0.038, and 0.163 larvae per m² of foliage. Results that describe or suggest similar densities during sparse intervals have been derived from several eastern Provinces and States (Allen and others 1986, Blais 1959, Crawford and others 1983, Dowden 1961, Fye 1963).

To my knowledge, no data have been accumulated in a life-table format for sparse populations of the jack pine budworm, and only a few life tables exist for the western budworm below about one larva per m². Some of these latter data have been summarized here (fig. 29). The others are summarized in Volney and Waters (1984). Nevertheless, four kinds of observations suggest that many western budworm populations persist at densities equivalent to those reported for the eastern budworm. First, from 1982 through 1990, densities of half-grown western budworm larvae were estimated annually as part of a silvicultural demonstration project on the Gallatin National Forest, Montana (Bousfield and others 1983, 1986). During these years, budworm densities have declined. Most recently (1988 through 1990), the insect population has remained below one larva per m² (fig. 49). Second, historical defoliation records reveal that this budworm has only caused visible defoliation in certain parts of its range, at least since 1947 (Kemp 1983). Third, biological evaluations have sometimes been conducted for the western budworm during intervals when the pest has been sparse. During one such interval, for example, Acciavatti (1973) used a sequential procedure to derive estimates of new egg masses in entomological units in Arizona and New Mexico. According to the procedure, a minimum of 50 branch tips (with a total foliage area of about 8 m²) were sampled in each unit (McKnight and others 1970). In the work summarized by Acciavatti (1973), no new egg masses were found in three of the six units from which summary records are reasonably complete. Fourth, even in areas with no defoliation history, pheromone-baited traps consistently catch moths.

Unfortunately, the dynamics of these sparse populations remain largely unknown. For the western budworm, extension from the PNW exclosure results (section 4.5.2) strongly
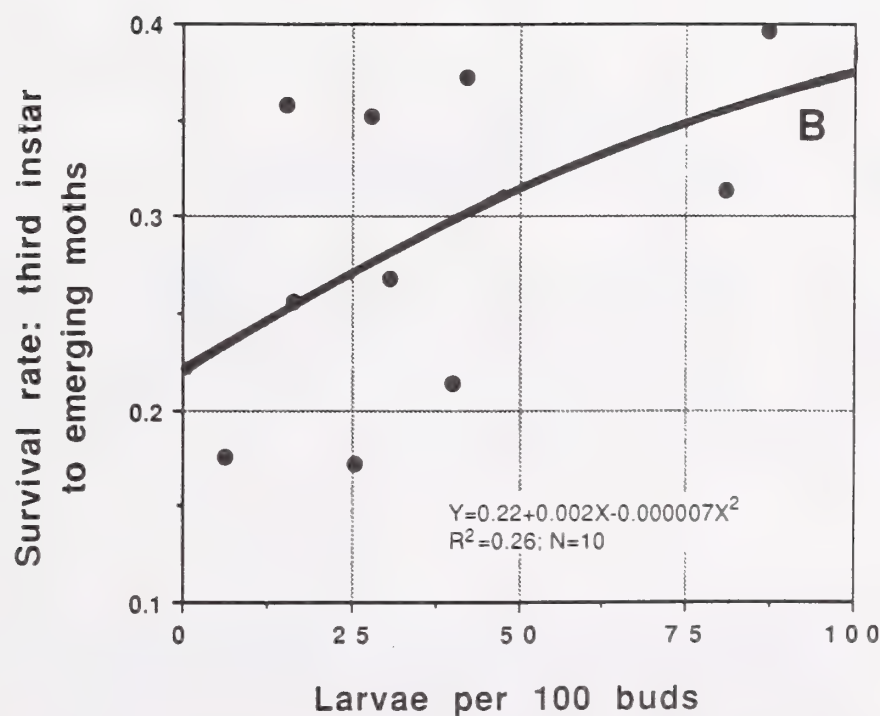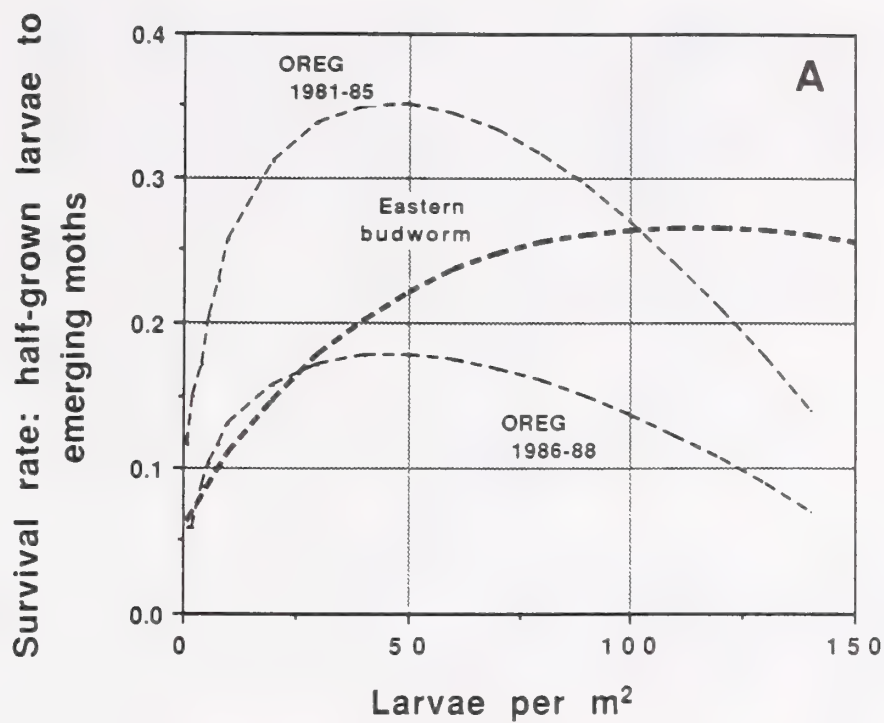
Figure 48—A. Density of fourth instars (if western budworm) or third instars (if eastern budworm) and survival rates to emerging moths; for eastern budworm, $S_L = 0.656 \cdot [0.096 + N_L \exp^{-(4.866 + 0.0090 N_L)}]$ (Watt 1963). In this equation, the survival rate of pupae has been set at 0.656. B. Jack pine budworm in Michigan (data from Foltz 1969; 1967 data only).

suggests that many such populations are dominated by predaceous birds and ants. Similarly, for the eastern budworm, Morris (1963d) postulated that sparse populations tend to be stabilized at innocuous densities by predators and parasitoids.

Working largely from information in Miller and Renault (1981), Royama (1984) disputes the notion that birds are important among low-density populations of eastern budworm, deducing that "...birds took a substantial number of budworm larvae and pupae when
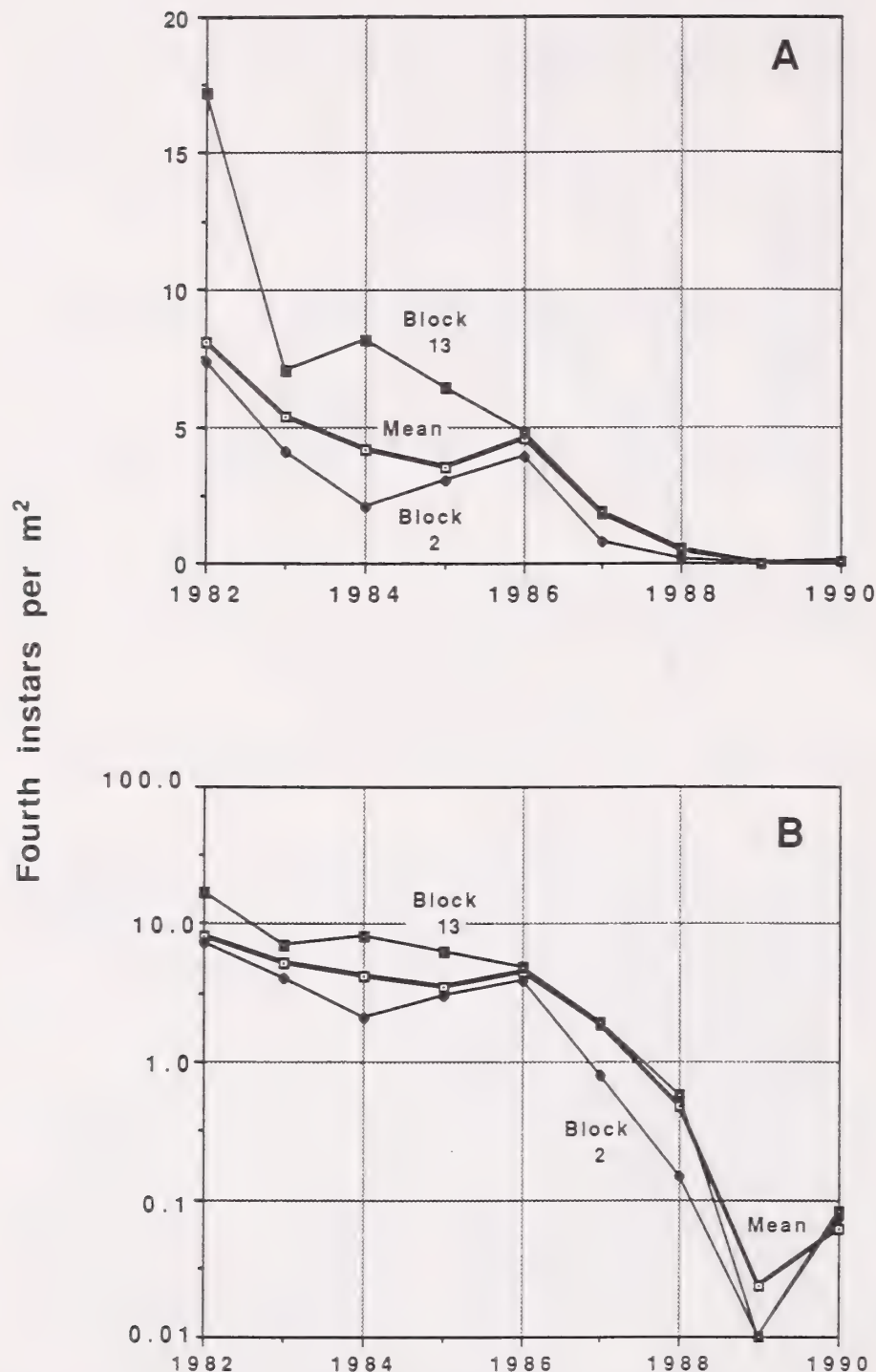
Figure 49—Annual trend in larval density of western budworm populations on the Gallatin National Forest, Montana. Samples were drawn from five blocks, with the highest densities usually found in block 13 and the lowest ones in block 2: A, arithmetic scale; B, logarithmic scale. To complete figure 49B, estimated mean densities equal to zero were arbitrarily set = 0.01 (adapted from data provided by L.E. Stipe).

insect density was high and ignored this source of food when the insect was scarce." In fact, although the trials conducted on a low-density population of eastern budworm by Miller and Renault (1981) are far from conclusive, I believe they show not only that predators were crucially important in maintaining this population at low densities, but also that the complex Royama described as "the fifth agent" was incidental at these low densities. Briefly, here is why.

For five consecutive years, Miller and Renault (1981) put about 100 young larvae (1 per cage) in fine-mesh cages designed to exclude both parasites and all predators (series 1

and 1A), and an equal number of larvae in wide-mesh cages designed to exclude birds but not smaller predators and parasites (series 2). These investigators also left about 200 larvae exposed (series 3). Each year, the trials were continued until all survivors became adults. Here are the results of these trials, expressed as an average survival rate from third instar to adults for the five years:

Trials exclude:	Starting larvae	Adult moths	Apparent survival rate
Macroparasites and all predators (series 1 and 1A)	388	256	0.66
Birds (series 2)	495	93	.19
Nothing (series 3)	694	7	.01

Unfortunately, the larger larvae in these trials tended to migrate from their feeding sites. Thus, much of the loss from both wide-mesh cages (series 2) and controls (series 3) was necessarily classified as "missing," and evaluation of predation by birds, specifically, was frustrated. Nevertheless, these results suggest the following:

- Larvae protected from both macroparasites and all predators (series 1 and 1A) were 66 times more likely to become adults than unprotected larvae (series 3).

- Larvae given some protection from predators (series 2) were 19 times more likely to become adults than unprotected larvae.

- Larvae protected from both macroparasites and all predators were about 3.5 times more likely to become adults than larvae given some protection from predators.

In a more recent study, Crawford and Jennings (1989) estimated that birds ate 84 percent of the late-instar and pupal eastern budworm in sparse populations in Maine and New Hampshire. From their 1989 estimates of fourth-instar density and an earlier estimate of branch surface area per hectare (Crawford and others 1983), peak larval densities in the sparse populations were between 0.85 and 1.82 larvae per m^2 of foliage. Thus, these results suggest that most of the insects classified as "missing" by Miller and Renault (1981) may have been eaten by birds.

4.7.4 Emerging Moths to Eggs

Royama (1984) provides a basis for examining observed egg production per emerging moth (Royama's E/M ratio = N_E/N_A) as a function of N_A in eastern budworm. Specifically, Royama used all of the Green River Project, New Brunswick, plots from 1955 and 1956 "...where data were available..." to provide a curve "...drawn by eye ..." that shows N_E/N_A as a function of N_A. To derive equivalent estimates for the western budworm, I assumed that mean EG = 40 (table 3, section 4.2), and modified equations that project egg masses as a function of emerging moths (section 4.6).

Figure 50A compares N_E/N_A as a function of N_A on a logarithmic scale in seven situations: eastern budworm in western New Brunswick in 1955 and 1956 and western budworm in six project-year combinations, ranging from IDA in 1980 to MONT in 1982. Equivalent data for jack pine budworm are also shown on a logarithmic scale in figure 50B. Arithmetic relations are shown for the three species in figure 51. For all three species, each emerging moth should deposit an average of 100 eggs "on site," if one assumes that: (a) half the emerging moths are females; (b) each female moth is capable of laying 200 eggs; and

A

MONT 82
NMEX 80
NMEX 79
NMEX 78
Eastern budworm
IDA 81-82
IDA 80

Emerging moths per m²

Eggs found per emerging moth

B

1966: Y= 177.8(X$^{-0.48}$); R^2=0.74
1967: Y= 63.1(X$^{-0.20}$); R^2=0.13
1968: Y= 37.2(X$^{-0.21}$); R^2=0.53

× 1967
○ 1966
■ 1968

Emerging moths per 100 branch tips
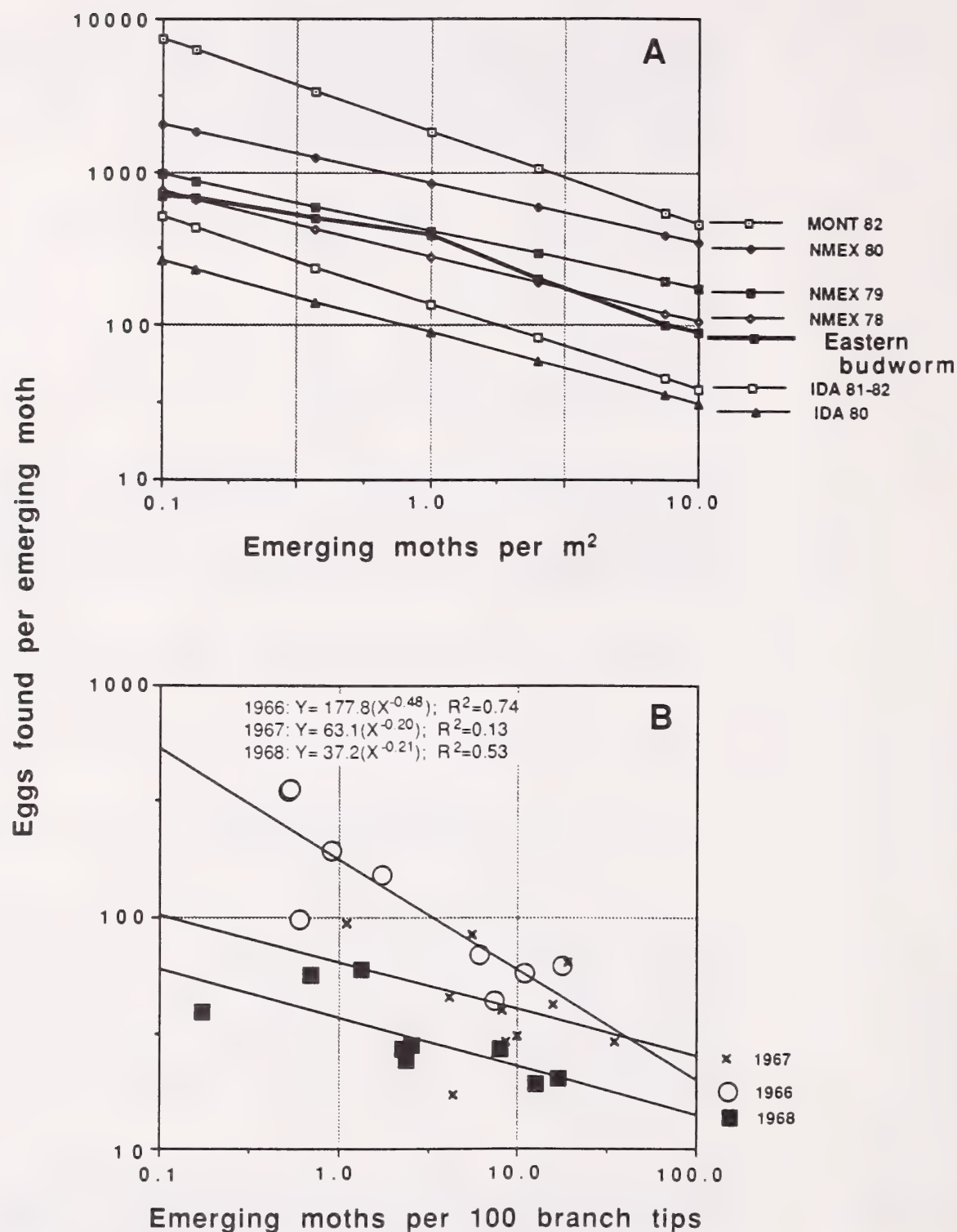
Figure 50—Emerging moths and subsequent eggs found per moth (logarithmic relations): A, western and eastern budworms (eastern budworm relation adapted from Royama 1984); B, jack pine budworm (data from Foltz 1969).

(c) no female dispersal or mortality occurs before oviposition is complete (each female moth deposits all her eggs locally). Clearly, more than 100 eggs were deposited per emerging moth in both eastern and western budworm populations when N_A was less than one per m², and a similar pattern occurred in the jack pine budworm.

Miller (1979) used population counts of eastern budworm female pupae, pupal cases, and egg masses that were recorded each year for 16 years (1960-75) from about 1,000 sample points in New Brunswick to derive mean egg to female moth (E/F) ratios in sprayed and unsprayed areas. He concluded:
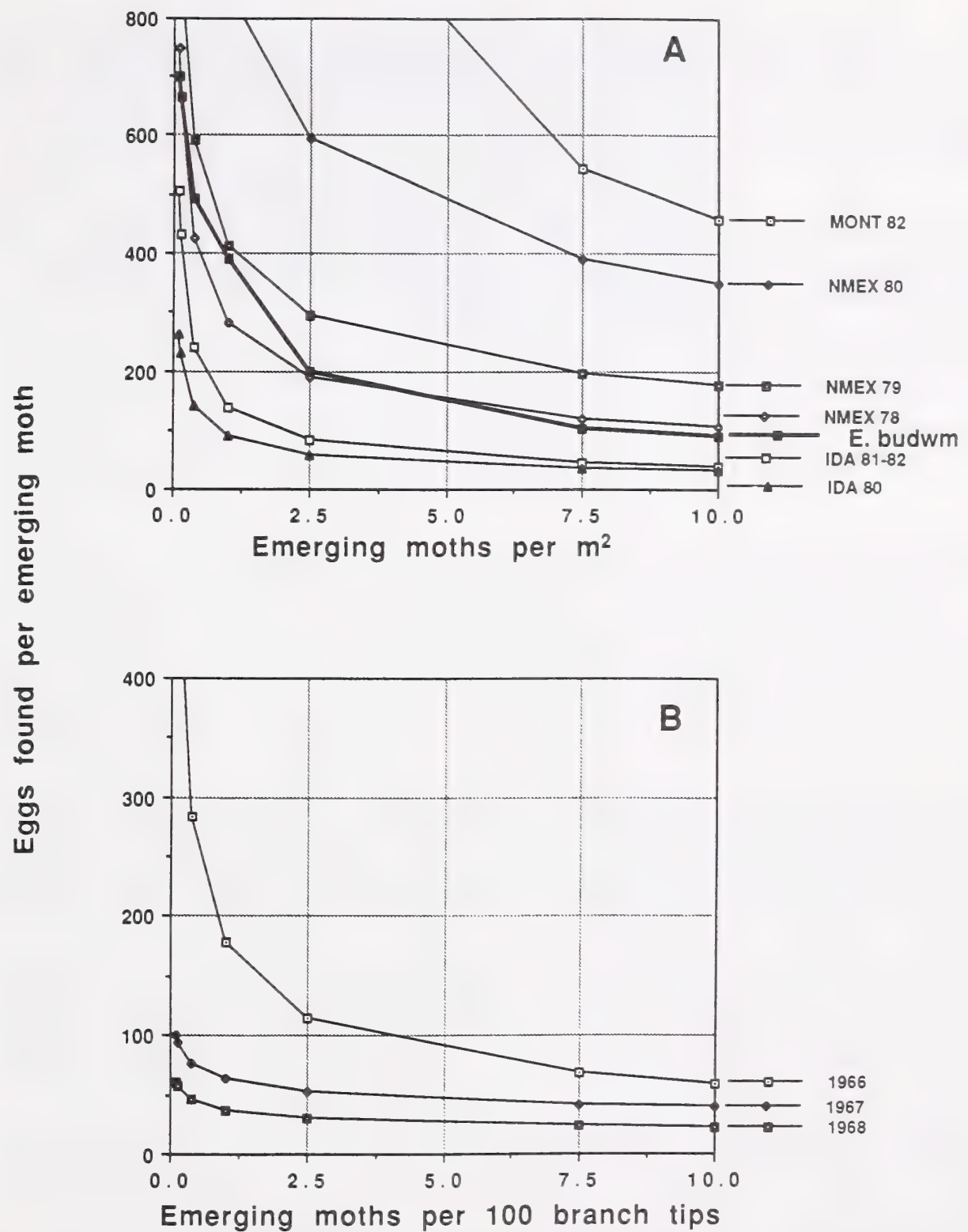
Figure 51—Emerging moths and projected subsequent eggs per moth (arithmetic relations): A, western and eastern budworms (eastern budworm relation adapted from Royama 1984); B, jack pine budworm (adapted from Foltz 1969).

The most evident change in E/F ratios occurred between years....[Mean] E/F ratios for unsprayed areas ranged from 29...to 276....[In equivalent sprayed areas, mean E/F ratios ranged from 51 to 430]...with the exception of 1963, a relationship was found between increasing size of infestation (size in t+1: size in t) and the E/F ratio recorded in year t in unsprayed areas....Ratios were highest where there was low female density...[and] no high E/F ratios were recorded at moderate to high female densities.

Three conclusions seem inescapable about egg production per emerging moth in the three budworms. First, in all species, this production (N_E/N_A) varied inversely with N_A.

Thus, within any given budworm generation, N_E/N_A in all species is strongly density-dependent, at least during outbreaks. Second, the curve used by Royama to describe this relation in the 1955-56 eastern budworm generations in the Green River Project is very similar to the 1966 generation of the jack pine budworm in Michigan, and virtually identical to the relations I derived for the western budworm in NMEX in both 1978 and 1979 (fig. 51). Third, the observations of Miller (1979), coupled with the relations summarized in figure 51, show clearly not only that E/M ratios in each of the three budworm species are density-dependent and similar, but also that the mean ratio in each species fluctuates across at least an order of magnitude from year to year. This topic is examined further in section 5.2.2.

5

Discussion

*In many cases,...grazing, population density, and nutrient cycling
provide the chief negative feedback mechanisms that contribute to
stability in the mature system....*

**—From "Fundamentals of Ecology"
by E.P. Odum (1971)**

5.1
Long-term Budworm-Forest Relations

By any measure, both the principal North American budworms and their hosts represent evolutionary success stories. If site occupancy is used to measure such success, a glance at range maps for the hosts of eastern budworm (Talerico 1984) clearly shows that some of these ranges are virtually transcontinental across the northern portion of the continent. Similarly, the ranges of the conifers that are hosts of the western budworm stretch across western North America from British Columbia to Mexico (Hermann 1987). Jack pine, *Pinus banksiana* Lamb., the principal host of the jack pine budworm, ranges from the eastern foothills of the Canadian Rockies east to the Atlantic Ocean and southward through the upper portion of the Lake States (Fowells 1965).

Like their hosts, the ranges of both the eastern and western budworms are enormous. According to Talerico (1984), the eastern budworm "...can be found from Virginia to Newfoundland, and west across Canada throughout the boreal forest region to the McKenzie River near 66°N...." In the West, the western budworm ranges from southern British Columbia south to New Mexico and eastern Arizona (Carolin and others 1987a). And the range for the jack pine budworm includes most of the range of jack pine (Harvey 1985).

5.1.1
Eastern Budworm

In New England, balsam fir "...is considered a subclimax type, except that it may be considered climax in the zone below timberline. It tends to become climax in Quebec and in the Lake States" (Fowells 1965). This fir is both the most common host and the one most likely to be killed during a budworm outbreak (Blum and MacLean 1984).

Compared to the other hosts of the budworm species, balsam fir is short-lived. For centuries, eastern budworm outbreaks have been occurring at more-or-less regular intervals (Blais 1965, Morris and others 1958b, Royama 1984). These outbreaks have typically been accompanied by extremely heavy balsam fir mortality in mature stands (Blum and MacLean 1984). Equally typically, this overstory mortality results in the establishment of new, vigorous stands (Baskerville 1975, MacLean 1988). In this sense, the eastern budworm has been viewed as "...a natural forest manager...." (Simmons and others 1984). Many authors (such as Coulson and Witter 1984) identify the eastern budworm as the most important insect pest in North American spruce-fir forests. In recent years, defoliation by this pest in eastern North America has sometimes covered an enormous area (Kettela 1983). In 1975, for example, it defoliated trees on more than 72 million ha (Hardy and others 1986). Recently, Volney (1989) labeled the eastern budworm "the most destructive pest of living trees on the continent."

Consistently, the overstory mortality that accompanies an eastern budworm outbreak serves to release advance reproduction. Because this reproduction already occupies the site, little if any advantage (in an evolutionary sense) would be gained for the short-lived overstory trees by investing in chemical defenses. Further, although evidence is conclusive that defoliators, including eastern budworm, respond negatively to increases in the raw fiber content of foliage (Baltensweiler and others 1977, Bauce and Hardy 1988), no evidence, to my knowledge, suggests that balsam fir trees vary systematically in their inherent tendency to increase this property in response to defoliation.

5.1.2
Western Budworm

Like balsam fir, the true firs that are major hosts to the western budworm (grand fir, white fir, and subalpine fir) are usually considered to be subclimax or climax species (although grand fir is seral in the upper, cooler, and moister parts of its range). In interior western forests, Douglas-fir is both climax and seral (Hermann 1987). Compared with balsam fir, all the western conifers that are hosts to western budworm are very long-lived.

Like those of its eastern relative, western budworm outbreaks have been occurring for centuries. Unlike the outbreak dynamics of the eastern budworm, however, the western budworm has shown no clear tendency toward either a distinctive outbreak duration or inter-outbreak interlude (Anderson and others 1987, Johnson and Denton 1975, Swetnam and Lynch 1989). Further, with few exceptions, relatively little tree mortality accompanies and follows outbreaks of the western budworm, and the mortality that has occurred has usually been more severe in regeneration and suppressed trees (Alfaro and others 1982, Fellin and others 1983). Unfortunately, the severe budworm outbreak that has been underway in the mixed conifer forests of eastern Oregon and Washington for the past several years appears likely to provide a major exception to this generalization. Often, outbreaks by this species can be likened to a thinning from below (Wulf and Cates 1987).

Although nonhost species in mixed stands can benefit from defoliation (Ferguson 1985), current projections do not suggest that defoliation by the western budworm will return budworm-susceptible stands to an earlier successional stage. In fact, results from the New Mexico Damage Assessment (Rogers 1984) suggest that the recent budworm outbreak in that particular area is probably accelerating changes toward more shade-tolerant species. In general, as Crookston (1985) noted, the effect of this defoliation is usually small compared to preconceived ideas. Thus, most budworm-susceptible stands can be expected to maintain site occupancy even in the presence of extraordinarily prolonged outbreaks. Clearly, these stands persist largely because western budworm survival declines drastically across the course of an outbreak. In possible contrast to effects in balsam fir, the evidence strongly suggests that these declines in western budworm survival are caused primarily by the formidable natural defenses of the host trees (section 5.2.3).

Regardless of the specific causes, stable long-term budworm-forest relations have apparently been characteristic in the life systems of both the eastern and the western budworm species.

5.1.3
Jack Pine Budworm

Jack pine "...is found on burned areas where there is little severe plant competition and where the soil is acid and has very good drainage and aeration....[The species] is one of the most intolerant trees in the region where it is native...it becomes more intolerant with an increasingly warm environment. ...[It] tends to give way to...more tolerant species, except on the poorest, driest sites....On...better sandy soils in northern Minnesota...usual succession is from jack pine to red pine, to eastern white pine, to...sugar maple, basswood, and northern red oak...[On poor sites] frequent fires...may [eliminate] jack pine and...[promote] northern pin oak and...other oaks. In parts of northeastern Canada, jack pine may be replaced...by white spruce, and in...eastern Canada it sometimes is succeeded by pure black spruce" (Fowells 1965).

Reports by both Clancy and others (1980) and Volney (1988) indicate that some areas have had more-or-less chronically high jack pine budworm populations for many years. Working with annual Forest Insect and Disease Survey reports of the Canadian Forestry Service, Volney developed a defoliation severity index for Manitoba and Saskatchewan

that spans 50 years. Volney found a weak 10-year periodicity in the outbreaks, which he attributed to a 10-year periodicity of years with a high incidence of fire (dry years). Such "fire" years tended to occur four to seven years before the budworm outbreaks. Because the periodicity in those records was derived from a weather pattern that is not likely to be repeated, Volney (1988) concluded that "...the correlation between outbreaks and a 10-year period is spurious." In any case, populations sufficient to cause serious defoliation seldom persist for more than two years (Volney 1989).

Kulman and others (1963) found that defoliation caused by jack pine budworm is accompanied by decreases in radial increment, some top-killing, and occasional tree mortality. Clancy and others (1980), however, reported that tree mortality after severe outbreaks can reach one-third of the merchantable volume. In view of the relative intolerance of jack pine, outbreaks by this budworm can be assumed to accelerate forest succession away from this host, at least in the absence of fire.

5.2 Population Processes

...the power of population is indefinitely greater than the power in the earth to produce subsistence....
—From "Population: the First Essay" by Thomas Malthus (1798)

The results presented in the preceding chapter raise many intriguing topics, some of which are discussed below. Because the literature on these topics is often fragmented and inconsistent, what follows is necessarily somewhat speculative.

In larger data sets, as many as 14 of the candidate independent variables were significant at $p = 0.05$. Consistently, however, a subset of three to five of these variables was associated with almost as much of the variation in any given dependent variable as was accounted for by the full set. Apparently, these key subsets reflect the action of one or more dominant processes in the budworm life system.

Results derived from projects that had both treated and untreated blocks (IDA, MONT, and NMEX) are summarized in table 27. As expected, prior budworm density was always an important predictor. In fact, density entered the model first or second in all 10 models summarized. After prior density, indices representing systematic differences from one year to the next and differences between treated and untreated plots were usually the second and third variables to enter.

After density, year, and treatment, only three other variables entered more than one of the reduced models: these variables are the indices of elevation, site wetness, and stand age, each of which entered two of the reduced models. Similar results were derived from regression models for all of the remaining projects, except that none of these latter projects involved insecticide treatment. Specifically, prior density entered most of these models first, and year effects usually entered second (Chapter 4).

The results clearly show that western budworm population dynamics are dominated by density-dependent processes and by those that vary systematically from year to year. In IDA, MONT, and NMEX, all areas with prior insecticide treatment, a dominant process was also related to those treatments. In addition, results derived from the WXBASE data show that weather phenomena were occasionally correlated with major changes in

Table 27—Order in which variables entered models[a]; results summarize reduced models in IDA, MONT, and NMEX (Tables 17-26)

Area	Dependent variable	Density	Year	TRT	EL$_{(i)}$	SLOPE	Aspect	WET	DOUG	TRUE	SPR	AGE	STK	HISH
IDA	N_L	1	2		3									
	DEF	1[b]	1	3						4				5
	N_M	1	2					4	3					
MONT	EG	1	2					3						
	N_L	1		2		4	3					5		
	DEF	1	2	3										
	N_M	1	2									3		
NMEX	N_L	2	5	1	3								4	
	DEF	1	2	4							3			
	N_M	1	2	3										

[a] Separate density strata (LO, MED, HI) have been pooled.
[b] The first term that entered included both density and year.

budworm numbers. Likely dominant processes in the western budworm life system are discussed in sections 5.2.1 through 5.2.3, and in section 5.2.6. Comparative relations among leaf-eating insects, their natural enemies, and their host plants in several eco-systems are discussed in section 5.2.4; life system responses to insecticides are described in section 5.2.5. Some possible reasons for the relatively minor and surprisingly erratic relations found between the budworm and many environmental attributes and indices are discussed in section 5.2.7; processes responsible for population modes and phases are summarized in section 5.2.8; and certain study implications are discussed in sections 5.2.9 and 5.2.10.

5.2.1 Density and Natural Enemies

"Who killed cock robin?" "I," said the sparrow, "with my bow and arrow, I killed cock robin."

—Nursery rhyme

Who killed cock robin is, for the most part, still a mystery.

—From "The Life of the Robin"
by David Lack (1943)

Equations (44) and (45) imply that western budworm survival from fourth instars to residual pupae will decline without bounds as N_L approaches zero. A principal use of the information described in this section is to provide a basis for modifying that scenario.

Using the results derived from exclosure trials, the effects of birds and ants are shown as a function of fourth-instar density, with this density displayed on both arithmetic and logarithmic scales (fig. 52A, B). On an arithmetic scale (fig. 52A) the effects of birds and
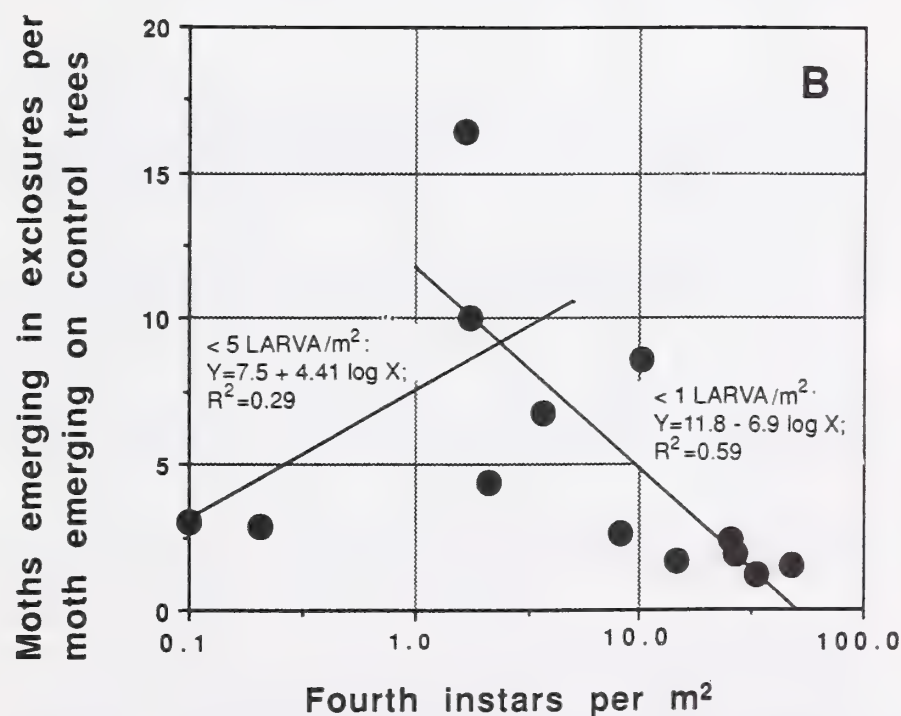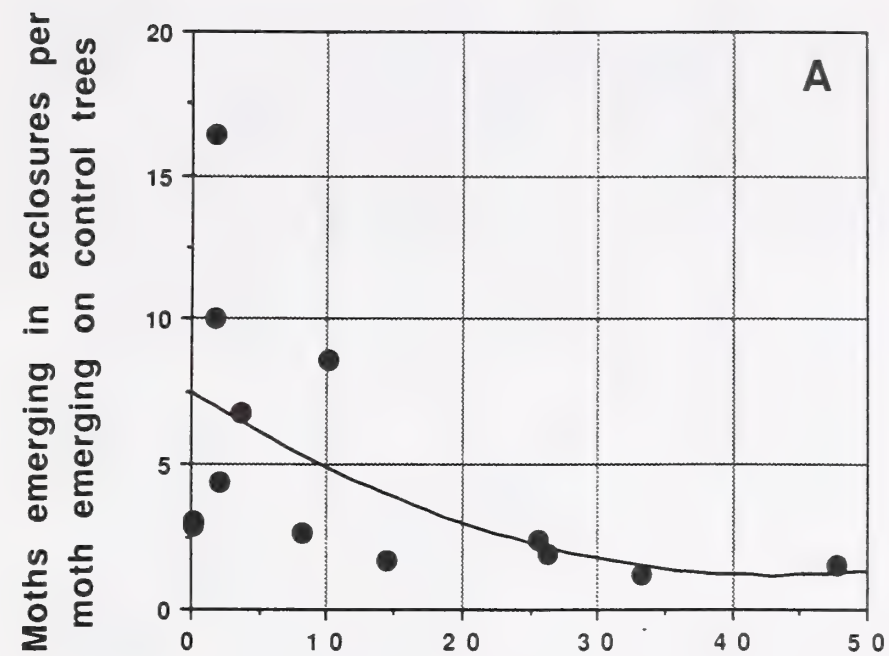
Figure 52—Fourth-instar density and effects of birds and ants on western budworm: A, arithmetic scale; B, logarithmic scale.

ants on the western budworm appear to increase to a maximum (about 7.5 moths emerging in exclosures per moth emerging on control trees) as N_L approaches zero. On a logarithmic scale, however (fig. 52B), the effects of these predators clearly reach a maximum at about one half-grown larva per m².

Both the survival rate projected by equation (44) (fig. 29) and the modification of that rate suggested by the exclosure results (fig. 52) are shown in figure 53. With figure 53 as a basis, budworm natural enemies are discussed below in four categories: (a) those that influence the population when N_L is below about 0.1 per m² (ultrasparse); (b) those

111
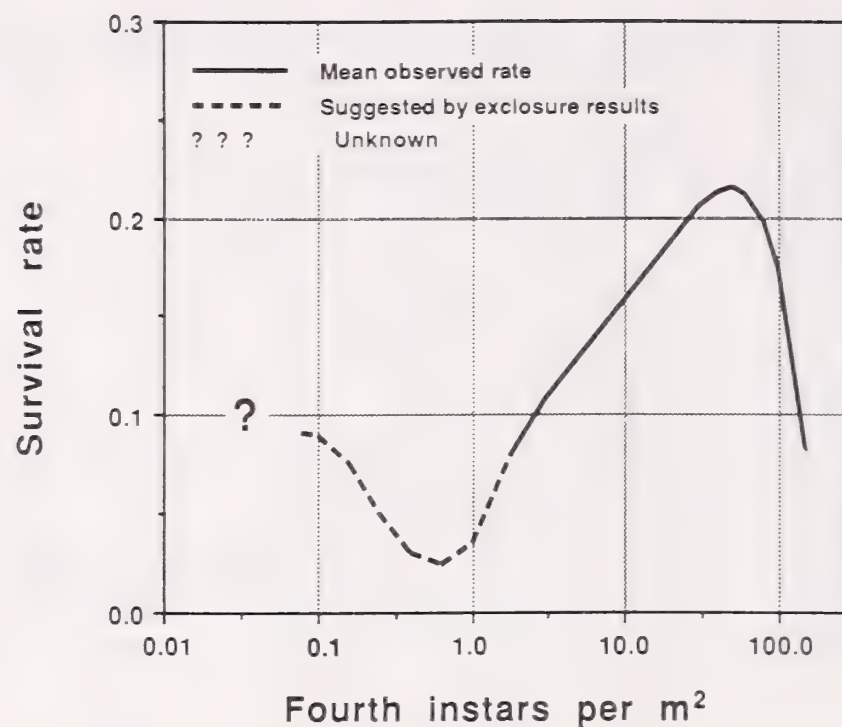
Figure 53—Fourth-instar density and western budworm survival to emerging moths. Above $N_L = 5$, the rate is a projection from equation (44). From $N_L = 0.1$ to $N_L = 5$, the rate is based on both equation (44) and the exclosure results shown in figure 52B.

that influence the population when N_L is between about 0.1 and 5 per m² (the dip); (c) those that influence the population when N_L is between about 1 and 50 per m² (incipient outbreaks); and (d) those associated with outbreak decline (declining outbreaks).

5.2.1.1 Ultrasparse—Although quantitative supporting data are largely unavailable, a substantial body of somewhat anecdotal evidence (Blais 1985, section 4.7.3.2) suggests that populations of both the eastern and the western budworm sometimes persist for many years below about 0.1 half-grown larvae per m²—a threshold that seems to elicit a strong functional response by birds and ants (section 5.2.1.2). Below that threshold, I suspect that spiders may play a particularly important role in budworm dynamics.

In fact, many successes of biological control do not confirm a need for close coupling between a pest and an associated control agent or agents (Murdoch and others 1985). Several authors—for example, Sailer (1971), Reichert (1974), and Messenger (1975)— have proposed that generalist predators may frequently be the most important natural enemies of low-density populations of herbivorous arthropods. More specifically, all of the conifer overstories inhabited by the budworm species considered here are also inhabited by remarkably similar groups of spiders (Allen and others 1970, Dahlsten and others 1977, Mason 1992, Moldenke and others 1987, Renault and Miller 1972).

Spiders have been described as"...extremely efficient prey-capture machines, largely resulting from their evolution under conditions of limited prey availability" (Reichert and Łuczak 1982). Further, spiders as a group are numerous. In fact, except during outbreaks of herbivorous insects, spiders outnumber all other arthropods (except mites) on the foliage of both balsam fir in the Eastern United States (Loughton and others 1963, Renault and Miller 1972) and Douglas-fir and true firs in the Pacific Northwest (Mason 1992).

Most of the work that relates spider predation to budworm populations has been con-

ducted on spiders and the eastern budworm. In a pioneering effort, Loughton and others (1963) used precipitin tests to demonstrate that about 20 percent of the spiders collected during a budworm outbreak in New Brunswick had fed on budworm. Subsequently, Renault and Miller (1972) used "planted" second instars on balsam fir branches to show that "...about 3 percent of the larvae survived on foliage with a spider predator (in these trials, *Dictyna phylax* Gertsch and Ivie), and 60 percent survived on the control foliage." Allen and others (1970) also report on limited feeding studies on spiders and the jack pine budworm. These authors reported that five of the more prevalent spider species "...closely approximated one another in their rate of feeding...[and that female spiders averaged]...0.4 late-stage larvae per day over a 10- to 40-day period."

Studies equivalent to those on spiders and the eastern budworm have also been performed using species drawn from western mixed conifers. Here, however, the Douglas-fir tussock moth was the prey species. Fichter (1984), for example, who used serological analyses, concluded that "...all spiders accept [tussock moth] larvae in direct proportion to the numerical abundance of tussock moth relative to total potential prey." Similarly, Mason and Paul (1988) used single-branch cages to estimate larval tussock moth survival on branches with and without a spider, *Metaphidippus aeneolus* (Curtis). Survival was 88.1 percent on branches without spiders. On branches with a spider, survival dropped to 13.3 percent. More generally, Moulder and Reichle (1972) found that spider predation during the spring on a forest-floor arthropod community was sufficient to balance accumulation of new prey biomass.

Where budworm density is below about 0.1 half-grown larva per m^2 of foliage, about 10 half-grown larvae per tree would be the maximum budworm density on an entire 10-m tall, open-grown host tree. Across such low budworm densities, I would not expect to find a detectable functional, numerical, or aggregative response by a natural enemy, with the possible exception of a highly specialized parasitoid. For this reason, possible responses by spiders and other groups to increasing budworm density will be discussed in following sections.

In conclusion, the information summarized here is compatible with suggestions by many investigators that spiders play a major role in determining the mean density of herbivorous pest insects including budworms during intervals when those pest populations are innocuous. In addition, Jennings and Crawford (1985) discuss many other predator groups (besides birds, ants, and spiders) that are also active in budworm-susceptible forests during these innocuous intervals.

5.2.1.2 The dip—Generally, exclosure trials with the western budworm support the view that "...natural enemies are a principal force in keeping populations of forest lepidoptera at low densities" (Mason 1987). More specifically, the results of these trials suggest that average survival in the age-interval from fourth instar to emerging moths (S_L) reaches a minimum at about one fourth instar per m^2 (fig. 53). Populations of both the eastern and the western budworms sometimes remain below this density for many years (section 4.7.3.2). This section describes relations between the budworms and the natural enemy groups that are thought to be important in maintaining these low survival rates.

Holling and others (1976) described a dip in the population growth rate of the eastern budworm at low budworm densities. They attributed this dip to "...avian predators, augmented by a degree of parasitism," and concluded that it represented a lower stable equilibrium, which would persist until "...that part of the curve rises above the replacement

line." Across a density range from about 0.1 to about 3 fourth instars per m^2, the exclosure results described in section 4.5.2 and summarized in figure 52 yield precisely the dip in the population growth rate of the western budworm that Holling and others (1976) projected for the eastern species (fig. 53). Undoubtedly, the relation between budworm density and this survival dip varies among places. More realistically, for example, the dip shown (fig. 53) should be visualized as a cross section through the "natural enemy ravine" of Southwood and Comins (1976). In any case, because the results in figure 52 are dominated by the influence of birds and ants, Campbell (1987) concluded that predation by birds and ants can maintain most budworm populations in the Northwest at sparse densities indefinitely, unless other processes upset low-density stability.

Birds and ants—Among the many avian predators of the western budworm, Langelier and Garton (1986) list 14 species that they consider "...dominant budworm-eating birds in mixed-conifer forests." Also, Garton (1987) lists 26 "important" avian species. And among the foliage-foraging ants in western forests, 13 species have been observed preying on the western budworm (Shattuck 1985, Youngs and Campbell 1984).

Although predaceous ants have not been identified as major predators of the eastern budworm, a wealth of information is available on the role of birds in the dynamics of this species (for example, Mook 1963, Morris and others 1958a). Jennings and Crawford (1985) reported that "...at least 49 species [of birds] have been observed with [eastern budworm] pupal remains in their stomachs." Most recently, Crawford and Jennings (1989) examined the stomach contents of birds taken from budworm-infested stands in Maine and New Hampshire. Budworm remains were found in 22 of the 25 species sampled.

Mattson and others (1968) found 28 species of birds attacking the jack pine budworm in Michigan. Both Allen and others (1970) and Jennings (1971) noted several species of ants that prey on this budworm in Michigan and Wisconsin.

Responses to increasing prey density—After an insectivorous bird has encountered a potential prey species several times, it may acquire a specific search image for that prey species (Tinbergen 1960). Similar "targeting" for a specific prey/host species undoubtedly occurs in other natural enemy guilds. Thus, as prey numbers increase, natural enemies may exhibit functional responses (changes in prey or host insects consumed or attacked per natural enemy), numerical responses (changes in number of natural enemies), or both (Holling 1966, Solomon 1949). In some life systems [for example, that of the larch sawfly, *Pristiphora erichsonii* (Htg.)], the prey is eaten almost exclusively by certain insectivores (in this instance, birds) during outbreaks (Buckner and Turnock 1965).

In eastern forests, most species of avian predators have not shown significant numerical responses to increasing budworm numbers (Crawford and Jennings 1989, Morris and others 1958a). In contrast, major increases in local densities of many bird species were noted as budworm numbers increased in the relatively heterogeneous mixed conifer forests of the Northwest (Takekawa and Garton 1984). Unfortunately, studies on responses to budworm gradations by the avian community in western forests are not adequate to separate the relatively transient aggregative responses by birds to locally abundant food from true year-to-year area-wide numerical increases in bird densities. Significantly, however, optimal foraging theory "...suggests that forest birds will exert the strongest stabilizing influence on highly profitable insects occurring in patchy environments" (Garton 1979), and changes in western budworm aggregation induced by predation (Campbell and others 1985) support casual observations that many predators of

this budworm are adept at locating and exploiting relatively dense prey populations in just such environments. Further, many species of avian predators in both eastern and western forests clearly exhibited major positive functional responses to increasing budworm densities.

Either birds or ants caused similar western budworm mortality in the absence of the other group (Campbell and Torgersen 1983, Campbell and others 1983b). Unfortunately, studies on budworm-eating ants in western forests have not been adequate to establish whether any of these colonial species exhibit major year-to-year numerical responses to a gradation in the western budworm. Further, the broader literature on this subject is sketchy and inconsistent. For example, Carroll and Risch (1990) assert that "...ants are capable of regulating in a facultative sense, their colony size in response to food levels." Horstmann (1977), however, concluded that wood ants, *Formica polyctena* Foerster, "...show neither a numerical nor a specific functional response to the changing abundance of their prey (the oak tortrix, *Tortrix viridana* L.)...."

Unlike this uncertainty, unequivocal evidence supports the view that "...the development of sociality has enabled ants to interact with their environment in ways unavailable to solitary insects. Group foraging and food sharing supply ant colonies with sufficient resources to support large populations, which in turn, through division of labor, permit the simultaneous performance of all the tasks a solitary insect usually performs sequentially" (Youngs 1983). Thus, through group foraging and intraspecific communication (Ayre 1968, 1969), ants sometimes showed spectacular functional and aggregative responses to increasing budworm density. Coupled with similar responses by birds, these findings support Readshaw's (1973) view that migration and searching behavior effectively apportion predators that possess these abilities relative to prey densities in a patchy environment. Certainly, the exclosure results support Hassell's (1978) conclusion that "...the differential exploitation of host patches as a result of parasitoids and predators aggregating in regions of high host density can be of the greatest importance to stability...."

5.2.1.3 Incipient outbreaks—From about 1 to 50 fourth instars per m^2, western budworm density and survival (S_L) increase together (figs. 29, 30). Significantly, similar direct relations between density and survival are also present in both the eastern budworm in New Brunswick and the jack pine budworm in Michigan (fig. 48). Further, an analysis of determination that was performed on pooled life tables representing the jack pine budworm in Wisconsin (Batzer and Jennings 1980) shows generally positive correlations between N_E and subsequent S_L. Thus, average survival rates among both the large larvae and the pupae of this species increase with increasing density.

If foliage quality determines the numerical behavior of western budworm populations at all densities, as asserted by Wulf and Cates (1987), then removal of budworm predators should have had little effect on budworm survival because increasing density should result in foliage responses that cause S_L to decline. In fact, however, when predaceous birds and ants were excluded, average S_L across this entire range increased to values that would undoubtedly trigger a full-scale outbreak, if these predator groups suddenly disappeared from a sufficiently large area (fig. 28).

Clearly, for all three budworms, the combined response by all natural enemies together is insufficient to keep S_L from increasing, once budworm densities pass a threshold somewhere near one half-grown larva per m^2 of foliage. Conversely, the gradual increase in mean S_L across this density range, both on trees with and those without birds and ants,

suggests not only that birds and ants continue to respond positively to further increases in N_L (above 1 larva per m²), but also that other natural enemy groups exhibit similar positive responses to increasing budworm numbers.

Birds and ants—Relations between eastern budworm density and bird predation displayed in Crawford and Jennings (1989) suggest that eastern budworm larvae and pupae consumed by birds in Maine and New Hampshire declined from near 100 percent of the population at about 60,000 fourth instars per ha (about 0.64 to 1.36 larvae per m² of foliage, in their plots) to about zero percent at about 3,270,000 larvae per ha (about 34.8 to 74.3 larvae per m²) (fig. 54B). In another study on the eastern budworm in Maine, Jaynes (1951) obtained somewhat similar results from small balsam fir trees, 1.8 to 3 m tall. In 1949, Jaynes stocked 12 trees with about 1,000 budworms each, by attaching egg clusters to the tips of branches. In May 1950, cheesecloth cages were placed over three trees, and three other trees were enclosed in 1/2-in (about 1.25-cm) mesh hardware cloth. Six trees were used as controls. In cloth-covered cages, mean S_L during 1950 was 0.703; in wire-covered cages, it was 0.175; and on control trees, mean S_L was 0.090.

Interestingly, the density-related trend in bird predation in Maine (Crawford and Jennings 1989) is roughly parallel to the one that represents the influence of bird and ant predation on the western budworm across densities ranging from 1 to 50 fourth instars per m² (fig. 54A,B). In the lower part of this range in prey density, however, much higher predation rates are projected for the eastern budworm. Undoubtedly, most of this apparent difference between the two life systems is merely a reflection of the different methods used in the two studies; specifically, the rates projected for the western budworm by the exclosure trials represent the irreplaceable (net) effects of the excluded predators (Campbell and Torgersen 1983). For the eastern budworm, Crawford and Jennings (1989) estimated a gross predation rate (a rate that does not account for the effects of mortality in the absence of birds). In addition, in stands where the eastern budworm was sparse, I suspect that many of the extremely high percentage-predation values estimated by Crawford and Jennings (1989) reflect the ability of these predators to locate and exploit slight aggregations of their budworm prey.

During 1980, the study on the western budworm with whole-tree exclosures was conducted on four sites in Idaho and one in Washington. Campbell and Torgersen (1983) reported from this study that birds and ants contributed an average of about 76 percent to total "killing power," or k (Varley and Gradwell 1960), during the budworm interval from fourth instar to emerging moths. During the subsequent year, 1981, equivalent records on exclosures and check trees were accumulated from two additional sites in eastern Oregon and three in western Montana. Here, results from all 10 sites in the four States have been pooled. Mean killing power contributed by birds and ants is 70.8 percent for the interval from fourth instar to emerging moths. At the time of these studies, these 10 sites were supporting budworm populations ranging from a low of about 0.3 to a high of about 48.3 fourth instars per m². Across this range of budworm densities, these collective results continue to support our earlier suggestion that mortality-causing factors other than birds and ants play a rather minor role in western budworm survival from half-grown larvae to emerging moths.

Spiders—The hunting spider, *Philodromus rufus* Walchenaer, is a common foliage-foraging member of the invertebrate community in the eastern boreal forest (Renault and Miller 1972). And in the West, this species is common on interior Douglas-fir and associated true firs (Dahlsten and others 1977, Moldenke and others 1987). Although
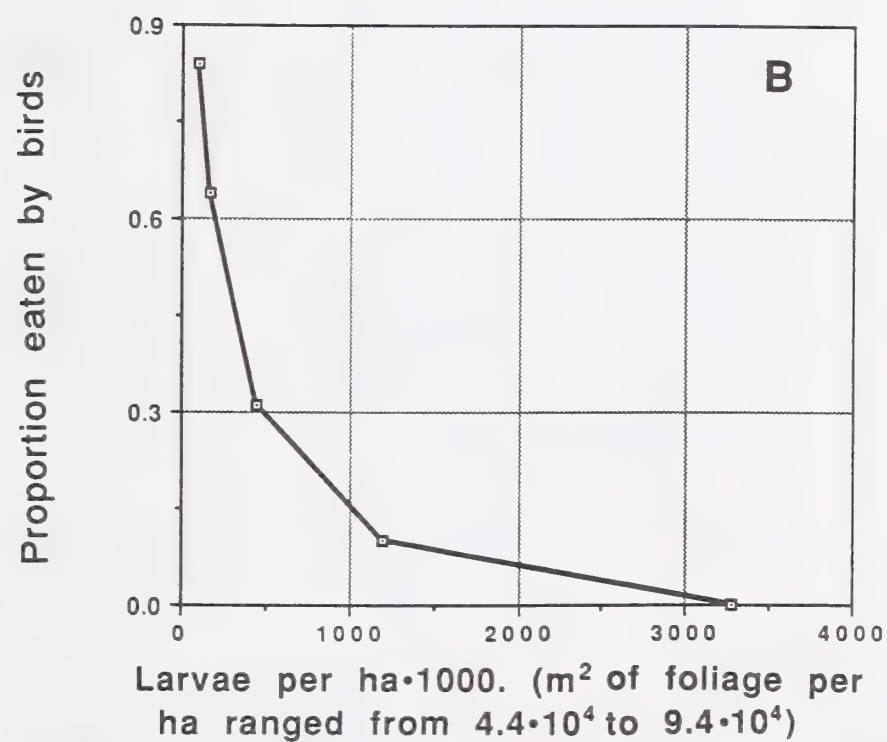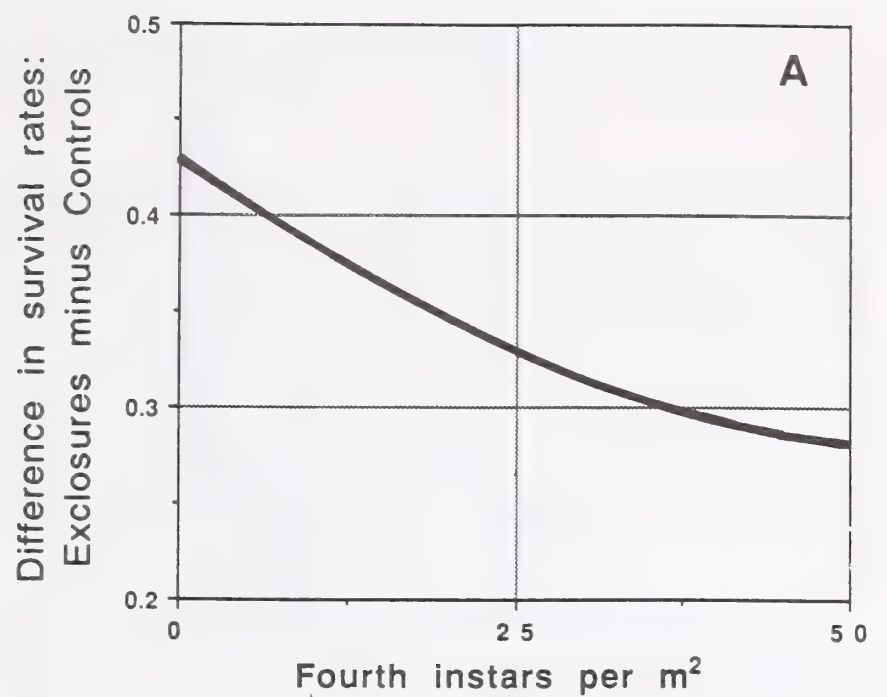
Figure 54—Density of half-grown larvae and the effects of certain predators:
A, effects of birds and ants on survival from fourth instar to emerging moths
in western budworm (derived from fig. 28C); B, effects of birds on survival in
eastern budworm (adapted from Crawford and Jennings 1989).

Allen and others (1970) did not encounter *P. rufus* on jack pine foliage in Michigan, they
often found *P. pernix* Blackwell.

In laboratory trials using *P. rufus* as the predator and *Drosophila melanogaster* Meign. as
prey, Haynes and Sisojevic (1966) found a relation between prey density and both pred-
ator searching time and feeding time. Thus, "...a typical functional response...became
evident for hungry spiders but not for well-fed spiders." Significantly, the sigmoid or

Type III curve (Holling 1959) that describes responses by this spider to this prey has been characterized as "...a powerful stabilizing mechanism in generalist predator systems..." (Hassell 1978).

Unfortunately, both aggregative and numerical responses by spiders to increasing prey densities are limited "...by intraspecific competitive effects...only a proportion of the individuals produced in a spider population are incorporated into the foraging unit because of intraspecific (territoriality) and predatory effects" (Reichert and Lockley 1984). In fact, although the size of territory defended by solitary spiders has been shown to vary with prey accessibility, solitary spiders show a spatial pattern between individuals that is far more regular than random (Burgess and Uetz 1982). Consequently, spider density has been characterized as "remarkably stable" over the years in any one biotype (Renault and Miller 1972), and spiders showed little evidence of a numerical response to a gradation in the eastern budworm (Watt 1963).

Parasitoids—Torgersen and others (1984) consistently found 14 species of parasites among rearings conducted as part of the PNW study. After examining parasitism among the PNW populations, these authors concluded that: "...parasitization contributed very little to variation in either [S_L] or S_G...these data indicate that...parasites may have a lesser role in the population dynamics of the western spruce budworm than previously thought." Similarly, Miller (1963b) concluded that "...parasites kill only a moderate proportion of the [eastern budworm] population [during an incipient outbreak] and a level of host density is soon reached where this proportion decreases...as host density increases.... [For] larval parasitism, this proportion is further reduced as severe defoliation changes the environment...." Also, Batzer and Jennings (1980) found little effect of parasites among the jack pine budworm populations they studied in Wisconsin.

5.2.1.4 Declining outbreaks—Declining values of S_L in OREG across the course of a western budworm outbreak (section 4.5.3.2) echo a similarly declining S_L in the eastern budworm during an outbreak in New Brunswick (Royama 1984). In this section, I discuss the possible roles of several natural enemy groups that have been implicated in causing budworm outbreaks to decline.

Birds—Predaceous birds have been identified as playing significant roles in terminating eastern budworm outbreaks (Blais and Parks 1964, Dowden and others 1950, Jaynes and Drooz 1952). And in the Northern Rocky Mountains, birds may have been important in terminating many incipient western budworm outbreaks during the first half of this century (section 5.2.8, fig. 55). I believe, however, that birds can only be expected to play a dominant role in terminating budworm outbreaks by showing major aggregative responses in situations where such outbreaks are localized. As Mattson and others (1968) noted for forests susceptible to the jack pine budworm: "In small forests...bird predation has greater potential...because nonresident birds can move into the...communities...and... add to the mortality caused by residents."

Parasitoids—To my knowledge, a report by Schmid (1981) is the only publication that documents the role of natural enemies during any of the prolonged western budworm outbreaks examined here. In that report, Schmid concludes that "percent parasitism... following spraying [in NMEX] showed a few increases and decreases but most [of the parasites] were not significantly affected." Nothing in Schmid's report suggests that any of these parasites played a dominant role in the dynamics of this population. Similarly, in his summary of natural mortality of a western budworm outbreak in COLO, McKnight
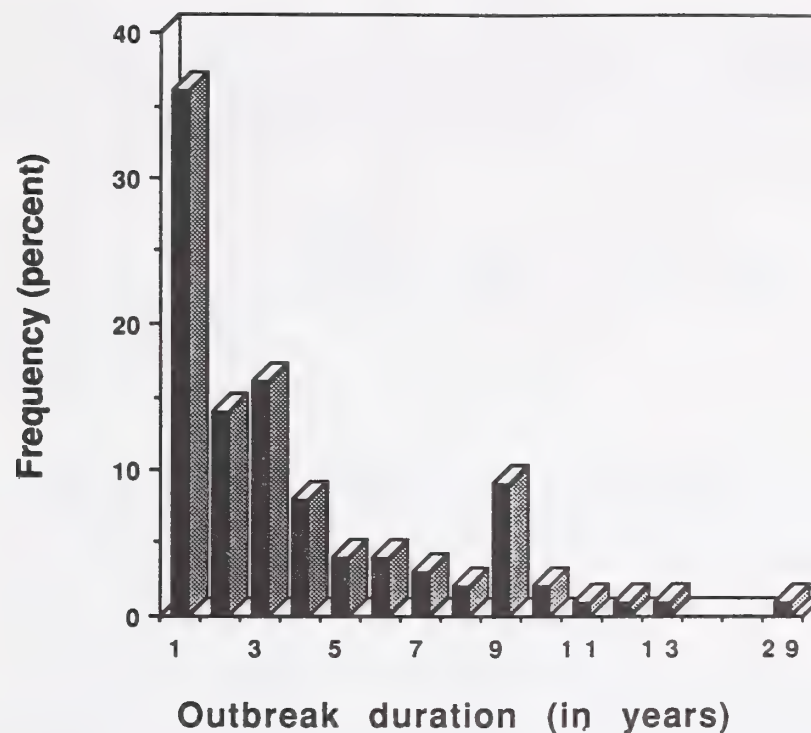
Figure 55—Outbreak duration in the American northern Rocky Mountains between 1922 and 1953; adapted from information in Johnson and Denton (1975). To derive this figure, outbreak duration on any given unit was defined as the consecutive years during which some defoliation was reported. By this definition, two single-year outbreaks could be reported in any given area in as few as three years.

(1971) was unable to show that natural enemies played a major role. Also, Harris and Dawson (1985) concluded that: "The sudden decline of the budworm...over the entire infestation [in British Columbia], regardless of parasitoid populations, suggested that parasitism was not a major factor."

In the East, Blais (1985) reached this conclusion about the parasites of the eastern budworm: "Generally, it is only during the final year of an outbreak that the action of parasites shows a pronounced increase. This increase is a symptom of the collapse rather than a cause...." Also, Allen and others (1969) reported that mortality of the jack pine budworm attributed to parasites was low during their Michigan study, but noted that parasites might hasten outbreak decline.

Pathogens—Both the extremely low survival rates in prolonged budworm outbreaks and the density-dependent nature of these rates are similar to mortalities known to have been caused by infectious diseases, primarily nuclear polyhedrosis viruses, in other defoliating pests, such as the Douglas-fir tussock moth, *Orgyia pseudotsugata* (McDunnough) (Mason and Thompson 1971, Thompson 1978, Wickman and others 1973), the gypsy moth (Campbell 1981, Doane 1970, Murray and others 1989, Podgwaite 1981), and the European pine sawfly, *Neodiprion sertifer* (Geoff.) (Griffiths and others 1971, Lyons 1964). Unfortunately, naturally occurring virus-caused epizootics "...have not been observed to date..." in populations of either the eastern or western budworm (Cunningham 1985), and Fellin (1983) concludes that "Pathogens do not appear to be an important factor in regulating western budworm populations...."

Certainly, the information discussed in section 5.2.3 provides sufficient reason to question whether the syndrome described by Royama (1984) as the fifth agent (section 4.7.3.1) is more a true primary cause of outbreak decline, or a symptom of decreasing foliage quality.

Other organisms—Many groups of natural enemies (besides birds, parasites, and pathogens) are known to flourish during budworm outbreaks. To my knowledge, however, none of these groups has been implicated as a major cause of outbreak decline in any of the three budworm species discussed here.

I have called this principle, by which each slight variation, if useful, is preserved by the term Natural Selection.
—From "On the Origin of Species..."
by Charles Darwin (1859)

For both western budworm and eastern budworm, several authors agree that the first batch of eggs is usually laid where the female moth emerges (Carolin 1987, Greenbank and others 1980). After that, the literature is scanty on factors that influence where and when a female western budworm will lay her remaining eggs.

Many of the relations described here (sections 4.6.3.7 and 4.6.3.8) suggest that site and stand attributes have a major influence on where female moths deposit their eggs. From these relations, several correlations between site and stand conditions and subsequent stand susceptibility and vulnerability (see review by Wulf and Cates 1987) seem likely to have their origin partially in the relative attractiveness of various sites and stands as oviposition sites.

5.2.2.1 Sources and sinks—Among the three prolonged outbreaks (IDA, MONT, and NMEX), average egg densities were highest in MONT (mean N_E = 1,547.5) and NMEX (mean N_E = 330.7) (table 3). In each area, average annual trend in egg density [$I = N_{E(n+1)}/N_{E(n)}$] was more than sufficient to maintain these high densities from year to year (in MONT mean I = 3.61; in NMEX mean I = 3.38). Thus at first glance, the budworm population in each area may seem to have achieved a significant rate of increase at an already high density.

According to Stoszek (1988): "It is apparent that...persistently high levels of insects...are indicative of forest ecosystems under stress from...nutrient limitations...." In fact, however, the persistent outbreaks in both MONT and NMEX were sustained largely by massive inflights of gravid moths. Average values of S_A in NMEX and MONT were 29.5 and 50.8, respectively (table 15). Because the sex ratio among emerging adult western budworm is usually about 1:1 (Campbell and others 1983c), reasonable estimates of the average number of egg masses deposited per emerging female in these areas are about 59 egg masses per female in NMEX and 101 egg masses per female in MONT. A female moth can deposit a maximum of only about five egg masses; thus, a reasonable conclusion is that inflight by gravid females is the only biological process that could account for this prodigious production of new egg masses.

Under reasonable assumptions of sex ratio, fecundity, and survival among emerging moths, the values of S_G in MONT and NMEX ($S_G = S_S \cdot S_L$ = 0.0026 in MONT and 0.009 in NMEX) suggest that both outbreaks would have declined dramatically without massive immigration. Thus, the prolonged outbreaks in both areas appear to have continued largely because they serve as sinks for gravid females from other source populations. In any case, the low values of S_S in both MONT and NMEX (figs. 7, 8) suggest that these host forests are well adapted to survive indefinitely even when massive moth inflights occur year after year.

Regarding mass flights of the eastern budworm, Royama (1984) wrote that "...there is no evidence...that invasions of egg-carrying moths...trigger outbreaks." Several other investigators, however, present findings that appear to refute Royama's conclusion. For example, Miller and others (1978) note that "...in New Brunswick (1952-1953) mean egg-mass densities, ranging from 20 to 30 masses/m², were recorded in areas sprayed with heavy doses of DDT that left few surviving residents." And Miller (1957) notes that 360 eggs were found in one lightly infested New Brunswick plot in 1953 for each 17 eggs that were expected—an approximate 21-fold difference. Similarly, Raske and Sutton (1985) note that "...all forested land [in Newfoundland] is inundated with moths when a massive moth flight has descended on an area..." Sippell (1984) presents defoliation maps for a portion of Ontario that show defoliation spreading in the general direction of the prevailing wind. More specifically, several authors suggest that immigration by the eastern budworm can cause a population to rise above a density where it can be controlled by natural enemies (Blais 1985, Clark and others 1978, Morris and others 1958b).

Qualitative changes—In a study of possible genetic changes related to dispersal, Mitter and Schneider (1987) reviewed the literature on the possible role of genetic change in the outbreak dynamics of insects. These authors concluded that "There is very little evidence of genetic change associated with outbreak episodes and certainly no conclusive demonstration that such changes influence population growth or decline.... In sum, the search for genetic effects on outbreak dynamics, in the absence of suggestive evidence like that available for the larch budmoth, is likely to be disappointing."

In contrast, I.M. Campbell (1962) found two different types of x chromosomes in the eastern budworm. "One...determines high basal metabolism, high food demand, slow larval development, large body size, high fecundity, and small egg size...the other...determines low basal metabolism, low food demand, rapid larval development, small body size, etc." He asserted that "...such sex-linked physiological-genetic diversity...not only facilitates but makes inevitable rapid and vast changes in...density...." (I.M. Campbell 1966). Further, Harvey (1977) found both higher eastern budworm survival and a higher proportion of eastern budworm female pupae reared from the third and fourth quartiles of the egg complement. Significantly, these are the eggs most likely to be deposited by migrating moths. Possible population consequences of such differences have not been investigated, to my knowledge, in any of the North American budworms. Similar but largely physiologically induced differences among individuals, however, have long been known to play a major role in populations of the western tent caterpillar, *Malacosoma pluviale* (Dyar) (Wellington 1957, 1965a). As Wellington (1980) noted "...the tendency to follow a nutritional pathway to differential dispersal is far more widespread among the insects than we had previously supposed."

5.2.2.2 Processes that trigger mass flights—According to Greenbank and others (1980):

> Emigration [of the eastern budworm] begins with an abrupt take off from the tree crown followed by the exodus flight upward from the canopy and across what Taylor (1958) refers to as the 'boundary layer' where the wind speed is less than the flight speed of the moth.
>
> Within the boundary layer, the exodus flight appears powerful, deliberate, and sometimes almost vertical...
>
> The causes of spruce budworm moth dispersal have not been identified: moths have not been seen emigrating from lightly infested and lightly defoliated stands....Exodus

flight is not an immediate stress response...females mate and lay about 50% of their eggs before leaving a site, even an adverse one. ...Emigration is not clearly density-related...**In mixed stands, spruce budworm moths emigrate just as readily from red spruce trees with 10% defoliation as from neighboring balsam fir trees with 90% or more of the current foliage removed**. (Emphasis added.)

A mass exodus of western budworm was not recorded in either DAMAG in 1981-83 (fig. 34) or MONT in 1983 (fig. 32). Nevertheless, the unusual relation between N_A and subsequent N_M in these plots during those particular years strongly suggests that a mass outflight did occur there during those particular years. In both instances, the unusual relation held over a wide area. Specifically, MONT covered 10 024 ha, and DAMAG included plots on each of three Ranger Districts.

In both MONT and DAMAG, each year of the presumptive mass outflight was preceded by at least two years during which observed values of N_M greatly exceeded the egg-laying potential of emerging moths. Partially in consequence, defoliation in both areas had been severe for several years in succession. Significantly, both Blais (1953) and Sanders and Lucuik (1975) presented laboratory data suggesting that starved eastern budworm females may disperse before ovipositing. Several authors have noted that adults of eastern budworm fly away from defoliated stands, presumably because these trees lack adequate oviposition sites (Blais 1953, Morris 1963b). Palanaswamy and Seabrook (1978) provide evidence that "Female moths may be capable of using pheromone concentration to assess population density and thus may be stimulated by the pheromone to lay a portion of their eggs and disperse."

As with the eastern budworm, the causes of mass outflight in the western budworm have not been identified. The pattern that has emerged, however, appears to include sustained prior defoliation. As Wilson (1975) noted: "The single most widespread response to increased population density throughout the animal kingdom is restlessness and emigration."

5.2.2.3 Distances that mass flights travel—Although the data presented here cannot answer questions about how far mass flights travel, they provide some leads. First, inflights are commonplace events in the western budworm life system; at least one such event is the only reasonable way to account for relations between N_A and subsequent N_M found during at least one year in IDA, MONT, NMEX, DAMAG, and OREG. Second, in at least one area (NMEX), the forested blocks were surrounded largely by nonforested lands for many miles in all directions. Nevertheless, this area was clearly subjected to a massive inflight of gravid moths in 1980 (fig. 33). And third, inflights can occur across areas at least as large as 30 000 ha. Even an area as large as 20 000 ha may be much too small to provide any meaningful clue that an inflight may be imminent.

In studies on mass flights of the eastern budworm in New Brunswick, Greenbank and others (1980) established that the airborne moths head downward, with an airspeed of about 2 m/s and an average wind speed of about 8 m/s at the flying height of the moths. "Thus, during a 35-min flight, the moths would average about 20 km, with 95% flying between 10 and 50 km. In flights of 1-2 h, moths would travel about 40-80 km." These authors found that the average duration of relatively short flights was 35 min. One-third of the flights, however, "...continued for 3-6 h, with a few moths sometimes flying until after dawn." Further, in what is probably an extreme example, Dobesberger and others

(1983) present evidence that large numbers of eastern budworm emigrated from New Brunswick to Newfoundland in July 1982, a trip that requires flying across 450 km of open water.

Together, these reports suggest that major flights by gravid western budworm females may travel much farther than has generally been supposed. Like its famous eastern cousin's, mass invasions of western budworm may occasionally have their origin in stands 200 km or more away.

5.2.2.4 Landing sites for migrating moths—According to Greenbank and others (1980):

> ...moths have been seen in the evening falling vertically into the canopy with wings folded. Similar descents have been observed after dark in the flashed beam of a signalling lamp. Before dark the ratio of descending to ascending moths is about 1:10 but nevertheless, thousands of descending moths have been seen through binoculars with over 80% descending in a rapid vertical drop while the remainder descended at angles of 30° or steeper.

> During the...observations, it seemed that **the landing of moths was being controlled and directly related to the presence of host trees**, with selection occurring from cruising heights of 100-200 m, followed by the observed plunging. (Emphasis added.)

Nothing in the results presented in section 4.6 on the western budworm is contrary to the discussion of eastern budworm immigration. In fact, relations found between S_A and the proportion of both Douglas-fir and other hosts in the western budworm (figs. 40-42) support the observation that landing eastern budworm moths may be "...controlled and directly related to the presence of host trees."

As previously noted, gravid western budworm moths both gravitate to stands with a high proportion of Douglas-fir and exhibit a higher efficacy of foliage conversion on a diet of this host than on a diet of the associated true firs (section 4.6.3.8). Similarly, the eastern budworm shows both a preference for ovipositing on white spruce over balsam fir (Jaynes and Speers 1949, Kemp 1981, Wilson 1963), and higher efficacy values on a diet of the former species (Koller and Leonard 1981). Further, Kemp (1981) found higher generation survival (S_G) on white spruce than on balsam fir.

In many life systems, insects respond to chemical cues to avoid overcrowding. As Prokopy and others (1984) noted, "By far the majority of known cases...involve [negative] reaction to pheromones or plant compounds emanating from occupied oviposition sites." Results in section 4.2.2.1, however, suggest that ovipositional behavior of the western budworm (as reflected by egg-mass size) is stimulated by a factor or factors related to either other moths, evidence of recent budworm activity, or both. Thus, in the life system of the eastern budworm, the ambient concentration of the sex-attractant pheromone produced by conspecific females appears to stimulate oviposition (Palanaswamy and Seabrook 1978).

Together, the above traits suggest that certain currently undescribed types of locales may serve as chronic "sinks" for gravid moths, even in areas characterized by large expanses of unbroken forest. For example, suppose that the landing of migrating western budworm moths is "controlled" by the presence of host trees. Städler (1974) concluded that females of the eastern budworm are "...stimulated to oviposit mainly by

chemical stimuli." Thus, this phenomenon could begin from moth responses to host stimuli such as those described by Atkins (1966) for the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins. Under this scenario, the windward fringe of a stand dominated by Douglas-fir might be particularly susceptible even though bordered by nonhost stands on its upwind side.

5.2.2.5 The foliage-eaters' defensive repertoire—Many attributes of foliage-eating insects appear to have evolved as defenses against natural enemies. A few such attributes are described here, primarily for species representing two different groups: conifer-eating budworms (tortricids) and tussock moths (lymantriids).

Budworms—Budworm populations exhibit behavior patterns that tend to minimize mortality from natural enemies on spatial scales that range from thousands of square kilometers to a single host bud or needle. First, flights by egg-bearing moths (sections 5.2.2.1-5.2.2.4) serve the population in several ways. On a large scale, mass outflights both relieve subsequent pressure on the host plants in defoliated forests and provide a way for an erstwhile sparse population that may receive these migrants to circumvent the high mortality rates among late instars and pupae that are associated with low budworm densities (section 5.2.1.2).

Second, intrastand patterns of egg-mass deposition by ovipositing western budworm moths show that the number of eggs per mass varies directly with egg-mass density (section 4.2.2.1). These patterns, which may be mediated by ambient western budworm sex-attractant pheromone (Palanaswamy and Seabrook 1978), undoubtedly reinforce both overdispersal when a budworm population is sparse and aggregations of insects when populations are dense.

Third, by hatching quickly, the various budworms minimize the dangers associated with aggregations of eggs. Later, through two periods of larval dispersal, they reinforce this disaggregation, both across a host stand and within a host tree.

Finally, by burrowing into host buds and needles, early-instar budworms effectively evade most of their natural enemies entirely, for several weeks. Later, by constructing and using silken feeding tubes, the larvae acquire some further protection from the tubes themselves. At the same time, by minimizing their intratree movements, the larvae tend to foil the sit-and-wait strategy that many species of spiders use to capture prey.

Tussock moths—Somewhat like for the budworms, spatial scales must be flexible in defining the population boundaries of at least one tussock moth—the gypsy moth. These insects sometimes erupt in massive outbreaks, where many independent innocuous populations may merge as parts of what Wilson (1975) terms a metapopulation. Although causative interpopulation processes in maintaining massive gypsy moth outbreaks remain obscure, such large-scale outbreaks have persisted in North America for as long as a decade (Campbell and Sloan 1978). More generally, multimodal numerical behavior has been described in a variety of animal populations (for example, Isaev and Khlebopros 1973, Peterman and others 1979).

At least one species of tussock moth is associated with budworm populations in both eastern and western spruce-fir forests. In the West, the Douglas-fir tussock moth is a well-known pest. And in the East, the white-marked tussock moth, *Orgyia leucostigma* (J.E. Smith) "...occurs commonly throughout eastern United States and eastern Canada

and feeds on a wide variety of deciduous and coniferous trees. Preferred hosts appear to include...larch and balsam fir" (Baker 1972).

Unlike the hairless budworms, one or more life stages of the tussock moths are covered with setae. In populations of the Douglas-fir tussock moth, setae from larvae and cocoons are known to cause both nonspecific irritations and allergic reactions (Martignoni 1978, Perlman and others 1976). Similarly, hairs from gypsy moth larvae and scales from the abdomens of adult female moths (which cover the egg masses) may also cause serious allergic reactions (National Gypsy Moth Management Group, Inc. 1991).

Buckner (1971) concluded that "...most forest vertebrates...are...highly discriminate in their choice of foods...." Not surprisingly, then, many of the generalist natural enemies of foliage-eating insects react differently to naked prey than to hairy prey (Otvos 1979), and Elkinton and others (1989), for example, reported that gypsy moth larvae were not a "major component" in the diet of any of the common bird species on their plots.

Galipeau (1975) described specialized ways several avian species use to "handle" gypsy moth larvae. A cuckoo, *Coccyzus* spp., for example, "...threads [the larva] through its mandibles several times prior to consuming it whole...to remove and break away some of the erect setae...." Galipeau also spent the entire 1971 field season observing the food-getting behavior of insectivorous birds in an oak-dominated stand near Eastford, Connecticut. At the time, that stand had been supporting an innocuous gypsy moth population for many years. Galipeau reported that the birds he observed consistently took naked larvae in preference to gypsy moth larvae whenever they had a choice. Similarly, in a western forest, Dahlsten and Copper (1979) reported that mountain chickadees, *Parus gambeli,* fed their nestlings many more naked larvae (geometrids, tortricids, pamphiliids) than hairy ones. And observations on the apparent reluctance of avian predators to feed on the white-marked tussock moth go back to at least the end of the 19th century (Howard 1897).

Despite the clear preference of birds for hairless prey, investigators have concluded that birds play an important role in the dynamics of low-density gypsy moth populations in many areas, including Japan (Furuta 1976), Germany (Luhl and Watzek 1977), Czechoslovakia (Turcek 1950), and the Soviet Union (Strokov 1956), as well as eastern North America (Smith and Lautenschlager 1981). An important role has also been attributed to birds in low-density populations of the Douglas-fir tussock moth (Torgersen and Dahlsten 1978, Torgersen and others 1990).

In North America, white-footed mice are common predators on gypsy moth larvae and pupae. As the insects develop, these mammals often exhibit an efficient way to eat portions of the larvae without ingesting the setae. The mouse holds each larva in its fore-paws and pulls off the head and upper gut with its teeth. Then it rolls the larval integument inside-out (like rolling-up a sock) and eats the inner tissues (Campbell 1975). Smith and Campbell (1978) report a variety of specialized techniques that other mammalian predators use when handling gypsy moth larvae. Smith and Lautenschlager (1981) also report that mice "...demonstrated a definite preference for hairless larvae...." in the laboratory. In any case, however, many investigators have concluded that small mammals play a dominant role in the dynamics of low-density gypsy moth populations—at least in eastern North America (Bess and others 1947, Campbell and Sloan 1977, Elkinton and others 1989, Smith and Campbell 1978).

To my knowledge, ants have not been identified as key predators of any of the lymantriids, although ant predation has been observed in Douglas-fir tussock moth larvae, pupae, and eggs, and in British Columbia "...'islands' of green trees surrounded by heavily defoliated trees were commonly associated with mound-nests of predaceous *Formica* ants" (Torgersen and Dahlsten 1978). Smith and Lautenschlater (1981) observed both *Camponotus pennsylvanicus* and *C. ferrugineus* eating gypsy moth pupae, and Campbell (1975) reported observations of ants removing and, presumably, eating gypsy moth eggs. Ants commonly destroy colonies of both the forest tent caterpillar, *Malacosoma disstria* Hübner, and the eastern tent caterpillar, *M. americanum* F. (Ayre and Hitchon 1968, Green and Sullivan 1950). Once the larvae reached a "certain size," however, "...their setae provide adequate protection against the ants...." (Ayre and Hitchon 1968).

Unlike the foliage-mining budworms, the tussock moths are always somewhat exposed to a wide range of natural enemies. That many of these species are somewhat cryptic is thus not surprising, especially during intervals when their populations are low. Sparse populations of late-instar gypsy moth larvae in eastern North America show such a strong tendency to rest and pupate in sheltered locations (Campbell 1975) that Campbell and Sloan (1976) suggested that this pattern had evolved primarily as a defense against foliage-foraging natural enemies in Europe. Similarly, Douglas-fir tussock moth larvae tend to pupate away from the foliage, and will use small wooden blocks for pupation sites (Dahlsten and others 1978). And in Connecticut, I noted that white-marked tussock moth larvae commonly rested and pupated under burlap bands that were being monitored as part of a study on gypsy moth population dynamics. I return to this topic in section 5.2.4.1.

5.2.3
Density and Induced
Host Defenses

[Acquired immunity theory]...predicts a fundamental cyclicity in the population dynamics of [leaf-eating] insects, which is determined by the induction and relaxation times of acquired immunity, but which is modulated in amplitude and exact timing by physical stress on the host plants.

—From "The American Naturalist"
D.F. Rhoades (1985)

The evidence strongly supports host responses to defoliation as a principal process in budworm dynamics during outbreaks of both the western budworm and the jack pine budworm. No evidence has been reported, however, that such responses play a role in determining stand susceptibility to the original outbreak. Under suboutbreak conditions, budworm survival increased dramatically with increasing density on trees protected from predators (fig. 28).

Dominant pathways leading to reduced budworm survival during outbreaks that are thought to operate through changes in the host trees are discussed below.

5.2.3.1 Early survival—Together, the magnitude and virtually ubiquitous occurrence of both density dependence and year-to-year differences in S_s in the western budworm and apparently in the jack pine budworm as well—but not in the eastern budworm (fig. 46)—lead me to postulate that the approximately density-independent survival rate in the non-outbreak PNW populations and the strongly density-dependent ones in prolonged outbreaks, such as those in IDA, MONT, and NMEX, represent approximate boundary conditions in a survival rate continuum for the western budworm (fig. 56). The rationale for this hypothesis is as follows:
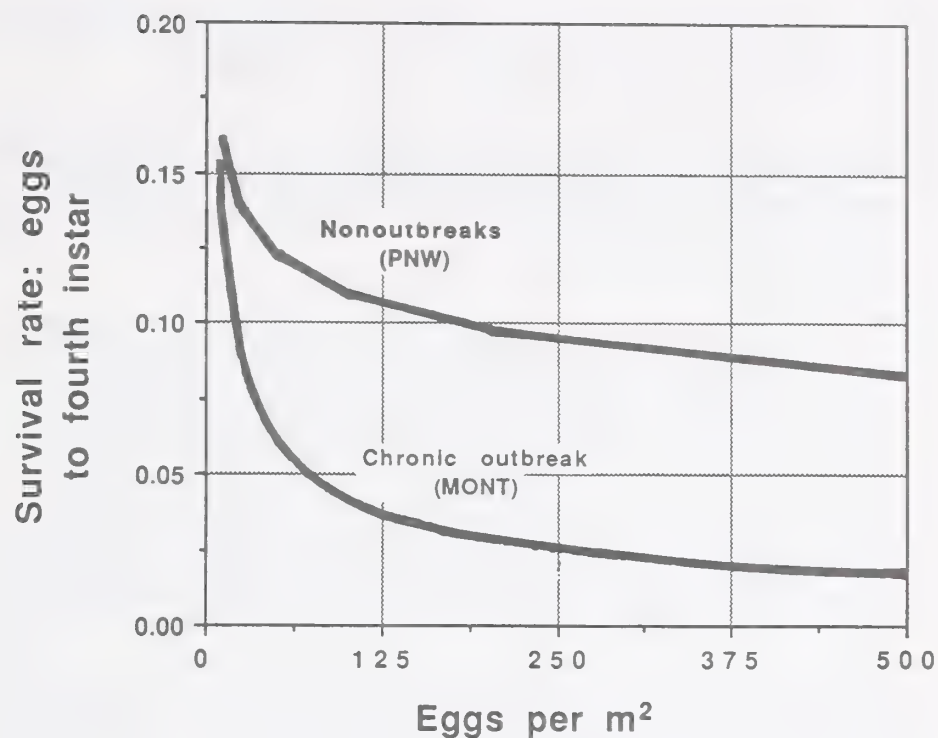
Figure 56—Egg density and survival rate from eggs to fourth instar in nonout-
breaks (PNW) and in a chronic outbreak (MONT).

Collectively, populations in IDA, MONT, and NMEX can be thought of as three points in a very large geographic range. Nevertheless, S_s exhibited a similar density-dependent relation to egg density in all three populations. An obvious thread linking these data sets is that all three were drawn from prolonged outbreaks. Thus, a strongly density-dependent S_s appears to be characteristic of such outbreaks.

Like the preceding data sets, the PNW data represent a large geographic area. Among these data, average S_s only decreased slightly across the available range in N_E. Among these populations, an obvious common feature is that they were purposefully selected to represent suboutbreak densities, but ones dense enough that statistically reliable samples could be derived at tolerable cost. Thus, a weakly density-dependent S_s appears to be characteristic among suboutbreaks.

If the above observations are linked, then S_s should change from a relatively high and weakly density-dependent rate at the onset of an outbreak to a relatively low and strongly density-dependent one as the outbreak progresses. Fortunately, the data from OREG are composed of counts drawn across the course of the most recent outbreak in eastern Oregon. When these data were analyzed, they yielded the pattern shown in figure 11. Clearly, this pattern reflects a systematic reduction in S_s across the past several years of this outbreak. Further, a similar pattern of declining S_s through time was exhibited by the new outbreak in DAMAG (fig. 9).

Most of the difference between S_s in nonoutbreaks and prolonged outbreaks appears to be determined in the interval between emergence from diapause and fourth instar. The following paragraphs show why.

Although budworm eggs may be infertile or subjected to mortality from natural enemies, average hatch was 93 percent among populations studied recently in the Pacific North-west (Torgersen and others 1984). High egg survival appears to be the norm in this

species. Similarly, mean survival to hatch was 0.812 in the Green River, New Brunswick, project on the eastern budworm (Morris 1963a).

Although Fellin (1981) reported that off-tree autumnal dispersal is minor in Montana, few estimates of fall dispersal have been made for the western budworm. After one intensive study of this interval, Eldridge and Egan (1983) found a survival rate of 0.39 on one site and 0.77 on another.

Both Eldridge and Egan (1983) and Terrell (1959) reported generally high and invariant survival of hibernating western budworm larvae in Oregon and Montana, respectively. Miller (1958) found a similar pattern for the eastern budworm in New Brunswick.

Spring dispersal begins as soon as the larvae emerge from hibernation. Fellin (1981) found that dispersal of second instars is extensive and occurred over several weeks. And results from north-central Washington (Beckwith and Burnell 1982) showed that some intertree dispersal continues until the larvae are well into their fourth instar. Losses during this period are almost certainly related to the energy reserves of the young larvae, which must find suitable food before these reserves are used up. For example, extended warm weather in the fall may critically deplete these reserves, as was found in populations of the eastern budworm (McMorran 1973).

In summary, there is no reason to suppose that survival during outbreaks is systematically lower than during nonoutbreaks from egg deposition in the fall to the end of diapause in the spring. Thus, the lower rates observed during western budworm outbreaks appear to be determined between emergence from hibernation and fourth instar.

The density-related patterns of early-instar survival in both the western budworm and the jack pine budworm are consistent with mortality-causing processes suggested in Perry and Pitman (1983). These authors used a laboratory colony of the western budworm to bioassay foliage from both westside Douglas-fir (var. *menziesii*) and interior Douglas-fir (var. *glauca*) from a "common garden," as well as foliage from mature trees of var. *glauca* that were growing in eastern Oregon. Foliage from the westside seedlings caused no significant larval mortality, but foliage from seedlings of var. *glauca* caused mortality ranging from no significant mortality to nearly 100 percent.

In addition to the above results, "...two year old foliage taken from mature *glauca* gave highly variable...results." In both 1981 and 1982, "...trees varied significantly in the larval mortality they produced....There was also variation in time. In one stand 9 of 10 trees produced higher larval mortality...in 1982 than in 1981" (Perry and Pitman 1983).

Regarding causal pathways, Perry and Pitman (1983) commented as follows:

> Although current theory holds that 'apparent' plants, which Douglas-fir surely is, should be primarily defended by digestibility-reducing compounds such as tannins and resins (Feeny 1976, Rhoades and Cates 1976), the larval-killing seen in our bioassays is probably not related to nutrition. Larval death was rapid (usually by the 3rd instar), rather than slow as would occur in starvation.

In considering causal pathways that may lead to density-dependent values of S_s, note that Perry and Pitman found larval-killing ability only in foliage one year old or older. This fact suggests that most of the killing took place when the young larvae tried to mine old

needles. Significantly, as density increases, an increasing proportion of the larvae emerging from hibernation will necessarily be forced to mine such needles, rather than buds.

Perry and Pitman (1983) also raised the following possibility: "The indication that selection for increasing tolerance may be occurring among budworm fed on killer-foliage ... raises the possibility that wild budworm populations may be well adapted to tree defense."

Results from IDA, MONT, and PNW (section 4.3.3.7), which show that S_s in those areas was directly related to stand age, support a suggestion by Wulf and Cates (1987) that defensive chemistry or nutritive quality of foliage may vary with tree age. They also echo findings relating eastern budworm outbreaks to mature fir stands that go back to Tothill (1919) and Swaine and Craighead (1924). In eastern budworm populations, high larval survival on old growth has been related to abundant flower production by the older trees (Bess 1946, Blais 1952), but investigators during an outbreak in northern New Brunswick (Mott 1963a, Greenbank 1963) could not show that S_s and the production of staminate flowers were positively related in that area and during that particular outbreak.

5.2.3.2 Late survival—Clearly, most of the density-dependent decline in larval survival that occurs during extended western budworm outbreaks has already happened before the larvae reach fourth instar. Nevertheless, like the declining S_s in OREG through time, values of S_L systematically declined from year to year in this same study (fig. 30). And like the systematic reductions in S_s, the declines in S_L appear to be primarily a function of decreasing foliage quality.

Cates and Redak (1988) reviewed work related to variation in terpene chemistry of Douglas-fir and its relation to the western budworm. Although they found that relatively resistant trees in one year remained relatively resistant during the following year, the terpenes they considered important were different each year. These authors concluded that "...[budworm] success is adversely affected when the pattern of terpene chemistry production significantly departs from the population average."

An increase in the raw fiber content of the needles might also have important consequences to the western budworm. Increases in this property in the foliage of larch have been shown to have an important negative effect on both larval survival and fecundity of the larch budmoth, *Zieraphera diniana* Guenée (Baltensweiler and Fischlin 1988). Also, Walters and Stafford (1984) reported that long-term defoliation of Douglas-fir by western budworm was associated with higher concentrations of soluble proanthocyanidins in the current year's needles. In any case, the systematic year-to-year reductions in both S_s and S_L across the course of an outbreak (figs. 9, 11, 30) are consistent with the idea that changes in foliage induced by defoliation represent defensive adaptations in the hosts of the western budworm similar to those suggested for responses by birch to defoliation by the geometrid *Oporinia autumnata* (Haukioja and Niemelä 1976).

Surprisingly perhaps, Piene (1980) noted increases in nutrient concentrations and needle weights in previously defoliated balsam fir trees. Nevertheless, changes in foliar quality deleterious to the eastern budworm can also be associated with defoliation. For example, Bauce and Hardy (1988) have shown that defoliation by the eastern budworm was related to increase in raw fiber, and that these increases resulted in lower pupal weight and larval survival. Clearly, much of the increased late-instar mortality from unknown causes found toward the end of an eastern budworm outbreak by Neilson (1963) and Raske

(1985), and termed "the fifth agent" by Royama (1984) could have been induced largely by such foliar changes. More generally, however, Mattson and others (1991) concluded that the host plants of the eastern budworm may have little or no active defense against this insect.

5.2.3.3 Interstand influences—Both the huge year-to-year differences in IDA in the relation between outbreak intensity (SIZ) and N_L (table 18), and the peculiar "pulsing" found in the WXBASE data in the relation between SIZ and $N_{M(n+1)}$ (equation [50]) are compatible with both the hypothesis that defoliation activates some sort of defensive response by the host trees and the fragmentary evidence for some form of communication between attacked and nonattacked plants (Rhoades 1983). At least, the close correlations between SIZ and both N_L and N_M in IDA (tables 18, 24) provide encouraging evidence that an underlying complex of area-wide processes may be important in budworm dynamics. Unfortunately, if other investigators have used indices similar to SIZ in population studies, I am not aware of the results of their work. Until equivalent results have been accumulated, speculating further on the nature of these processes would be premature.

5.2.3.4 Systematic differences among areas—Comparison among the western budworm survival rates shown in figure 46 strongly suggests a systematic west-to-east difference in S_s during outbreaks. Starting from 100 and 400 eggs per m^2, for example, here are projected values of S_s during outbreaks in both the westerly populations (OREG and IDA) and those farther east (MONT, NMEX, and DAMAG):

S_s projected from:

Area	100 eggs per m^2	400 eggs
OREG (1985-88)	0.222	0.070
IDA (1980-81)	.228	.088
MONT (1981-83)	.041	.019
NMEX (1977-79)	.079	.047
DAMAG (1980-83)	.082	.035

Together, these results show that the westerly populations consistently produced several times more half-grown larvae per egg than their more easterly counterparts. I think this pattern suggests a west-to-east increase in the inherent ability of interior Douglas-fir (and, possibly, other host species) to respond to budworm outbreaks.

Certain management implications arising from these results are discussed in section 5.3.3.

**5.2.4
Density and the
Herbivore Community**

Three viewpoints have dominated perceptions of causation and behavior. Each suggests distinctly different policies and actions. The first is an equilibrium-centered view that emphasized constancy in behavior over time. The second is a dynamic view that emphasized the role of instability in the maintenance of system resilience. The third is an evolutionary view that highlights change and the surprises generated by such change.

—From "Perceiving and Managing Complexity"
by C.S. Holling (1984)

About 40 species of lepidopterans have been associated with the western budworm in buds or on new shoots (Carolin and others 1987b, Stevens and others 1984). And even during a budworm outbreak, these associates may constitute as much as 48 percent of the total larvae and pupae found (Markin 1982). No doubt, an equivalent complex of foliage-eating insects is associated with every major terrestrial vegetational type. Consequently, one may wonder about possible relations among defoliators such as the budworms, their various communities of natural enemies, their herbivorous associates, and their hosts.

5.2.4.1 Natural enemies—Given a choice between a budworm and a tussock moth or other hairy insect, many generalist natural enemies of these herbivores will consistently opt for the budworm (sec. 5.2.2.5). At least superficially, then, a budworm outbreak appears to present a "window of opportunity" for many of their herbivorous associates to increase dramatically. Because small budworm larvae are protected in buds and needles, however, a budworm outbreak may actually result in increased pressure on their more exposed associates. In any case, simultaneous outbreaks of budworms and any of their associates have been rare.

In contrast, gypsy moth outbreaks are fairly likely to be accompanied by high densities of other defoliators (usually, tent caterpillars, but also a variety of loopers), as suggested by Eggen (1987) and my own observations. More dramatically, outbreaks in northern hardwood stands by the saddled prominent, *Heterocampa guttivitta* (Walker), rarely occur alone. Such outbreaks are usually accompanied by high densities of a variety of other foliage-eating species (primarily naked larvae [geometrids, other notodontids, and a saturniid], but also, on occasion, the white-marked tussock moth) (Allen 1987, Magasi and others 1978). Those observations are compatible with evidence that birds depress the already low abundance of a variety of foliage-eating insect species on patches of striped maple, *Acer pensylvanicum* L., a major understory component of northern hardwoods, and thus may act as low-density population regulators (Holmes and others 1979). By extension, the multispecies nature of defoliator outbreaks in such stands suggests that relaxation of pressure by this group of natural enemies may simultaneously release many foliage-eating species.

After two or three outbreak years, starvation and disease bring an end to saddled prominent outbreaks (Miller and Allen 1979). Interestingly, Allen (1991) also reports that all other erstwhile numerous leaf-eating associates are also rare during the following year. Again, this observation is compatible with the notion that generalist natural enemies can be particularly effective during outbreak declines.

5.2.4.2 Interspecific competition—A commonly accepted view is that competition for food among species with very similar environmental needs will lead sooner or later to the local extinction of the species with inferior competitive ability (Gause and Witt 1935, Hutchinson and Deevey 1949, MacArthur 1958). Various foliage-eating insect species do compete fiercely in the rather rare instances where food is clearly limiting. For example, predation by larvae of the spruce coneworm, *Dioryctria reticulella* (Grote), on the western budworm "...can be expected to increase when...new foliage is scarce" (McKnight 1971). Despite such interactions, the simultaneous occurrence at high densities of several foliage-eating species does not support suggestions that interspecific competition among herbivores commonly limits herbivore species abundance.

5.2.4.3 Host defenses—As Myers (1988) noted, "Rather than representing a tightly coevolved system, the defense system of plants represents a general adaptation to many 'elicitors.'" Thus, whatever defenses plants may have evolved against herbivory, it is reasonable to suppose that defenses triggered by defoliation that may have been caused primarily by one herbivore will adversely influence survival of many herbivorous associates. Clearly, this notion is compatible with the observation that most budworm outbreaks are not accompanied by outbreaks of their foliage-eating associates.

5.2.4.4. Ecosystem resilience—Density-dependent control by natural enemies is clearly paramount in maintaining low populations of foliage-eating insects. At higher densities (during outbreaks of the western budworm, for example), the evidence suggests that the usually much lower densities of this pest's foliage-eating associates may continue to be regulated largely by natural enemies, coupled with heightened host defenses. In other life systems, during outbreaks of the saddled prominent, for example, the evidence suggests that the high densities of both this insect and many of its herbivorous associates may continue to be regulated primarily by natural enemies.

By extension from the differences just described, northern hardwoods may not have been exposed to major selection pressure by defoliators. If this is true, these northern hardwood hosts may not have evolved effective defenses against foliage-eaters. Under this scenario, two catastrophes could occur if natural enemies of the defoliators suffered a calamitous decline. First, the stands would be devastated. Second, competition for food would eliminate many species of the foliage-eating guild.

Unfortunately, even qualitative information is sketchy in this complicated area of community dynamics, and quantitative information can only be assembled through further research.

**5.2.5
Life System Responses
to Insecticides**

*...bacterial insecticides may be one important answer to the problems
of such forest insects as the budworms and the gypsy moth.*
**—From "Silent Spring"
by Rachel Carson (1962)**

Reduced budworm survival during posttreatment years in areas treated with an insecticide could operate through changes in (a) some natural enemy or natural enemy complex, (b) the budworm population itself, or (c) the host trees.

5.2.5.1 Insecticides and natural enemies—Studies in mixed conifer forests in eastern Oregon showed that both carbaryl and acephate have adverse effects on foliage-foraging ants (Murphy 1985, Murphy and Croft 1990, Shea 1978). Also, although depressed brain

cholinesterase (ChE) was found in only two Cassin's finches, *Carpodacus cassinii* Baird, after application of carbaryl in one study in mixed conifer forests in eastern Oregon, significant depressions in brain ChE were found in several species of insectivorous birds after applications of acephate (Shea 1978). Despite such possible posttreatment reductions in natural enemies, budworm survival rates were significantly lower in treated blocks in all three of the insecticide treatment projects.

5.2.5.2 Insecticides and population quality—In recent papers (Robertson and Stock 1985, Stock and Robertson 1980), comparisons of response to pesticides among groups of western budworm showed that responses among populations varied as much as 18-fold, and that these differences in response have a genetic basis.

Clearly, differential responses of the magnitude found by Robertson and Stock could be linked to factors that would provide a genetic basis for the differences in IDA, MONT, and NMEX between the plots on treated and untreated blocks, at least during the first posttreatment year. As previously noted, however, the plots in all three of these areas were subjected to inflights. At least in MONT and NMEX, these inflights were so massive that they would necessarily dilute any genetic shift very rapidly. Nevertheless, the difference between the plots in treated and untreated blocks did not diminish during the period covered by these three studies, at least during the first several posttreatment years. Clearly, the difference between treated and untreated blocks in NMEX did not disappear until at least the seventh posttreatment year (figs. 24, 38).

5.2.5.3 Insecticides and host responses—I have been unable to find empirical evidence against the hypothesis that the difference in budworm survival between treated and untreated blocks is a function of differential responses by the host trees in the two situations.

If the hosts of the western budworm defend themselves against attack, then resources allotted to these defenses are probably maximal in places where the stand has been under attack for several years. In such outbreaks, the resources available to the trees must have been diminished by the attacking pests. Thus, any respite from attack, as could be expected in the year of a suppression project, would provide the trees with additional defensive resources. Although this scenario is speculative, it provides a rationale for the low posttreatment survival rates of the budworm in IDA, MONT, and NMEX.

In contrast to the low posttreatment western budworm survival, the eastern budworm populations studied by MacDonald (1963b) exhibited exceptionally high posttreatment values of S_s. Significantly, the treated western budworm populations were in areas characterized by prolonged outbreaks, and the treated populations of the eastern budworm studied by MacDonald were in an outbreak that was still new. More recently, Fleming and others (1984), who used records collected by the Maine Forest Service, showed that spraying in a sustained eastern budworm outbreak had a greater depressing effect on defoliation in the year after treatment, rather than in the treatment year. Also, Dimond and Morris (1984) noted that both B.t. and chemical insecticides may work more effectively against the eastern budworm "...after a budworm outbreak has persisted in a region for several years." These authors suggested that one responsible factor may be a microsporidian disease. Results presented in Bauce and Hardy (1988) show that increases in raw fiber content as a result of prior defoliation by the eastern budworm could also be a major factor contributing to an apparent increase in pesticide effectiveness.

*The destruction wrought by storm, low or high temperature, or other
weather conditions, is to be classed as catastrophic, since they are
wholly independent in their activities upon whether the insect which
incidentally suffers is rare or abundant*
—From "The Importation into the United States of the Parasites
of the Gipsy-moth and the Brown-tail Moth"
by L.O. Howard and W.F. Fiske (1911)

The results in sections 4.3.3.8 and 4.6.3.9 show that biologically significant and, occasionally, drastic changes in budworm numbers were correlated with particular weather phenomena. Some processes that might account for these statistical correlations are discussed below.

5.2.6.1 Temperature—Results from WXBASE (section 4.3.3.8) suggest that extreme cold in midwinter can be lethal to hibernating larvae, but that early emergence from diapause (induced by mild temperature during March) may also be associated with low subsequent survival. In addition, these results support both Hard and others (1980), who reported that defoliation trend in western Montana varied directly with mean maximum temperature during May, June, and July of the preceding year, and Greenbank (1956), who found that "larval development [of the eastern budworm] is more rapid in dry and sunny weather."

Undoubtedly, some of the low springtime temperatures in WXBASE were associated with frosts that were severe enough to result in direct budworm kill. One such spring frost has been reported for Montana budworm populations by Fellin and Schmidt (1973).

Apparently, below-average spring temperatures continue to depress subsequent budworm numbers even when these temperatures are sublethal (fig. 15). One possible reason for these results is suggested by I.M. Campbell (1989). He fed western budworm larvae on foliage he had collected and frozen for five successive years from balsam fir, *A. balsamea* (L.) Mill., at the same stage of development from a stand near Desbarats, Ontario. He found that pupae were about 20 percent heavier when larvae had been fed foliage produced in early compared to late spring seasons. Campbell estimated that this weight difference, which he attributed to an influence of climate on host-plant quality, could result in a 25-percent difference in female reproduction rates.

5.2.6.2 Precipitation—Budworm survival was inversely correlated with the average amount of precipitation during rainy days in May. This correlation suggests that the dispersing larvae may be particularly vulnerable to the mechanical effects of rainfall. Not surprisingly, Lucuik (1984) found that "...both prolonged rain and freezing temperatures during and shortly after emergence [of second instar eastern budworm]...may...have a profound impact on outbreak development."

Several investigators (Greenbank 1956, Ives 1974, Pilon and Blais 1961, Wellington and others 1950) have concluded that outbreaks of eastern budworm are often preceded by several consecutive dry summers, and both the results in section 4.3.3.8 and those in section 4.6.3.9 show that western budworm survival was highest during moderately droughty spring and early summer seasons. Interestingly, budworm survival in the chronically droughty Montana sites was diminished during exceptionally dry weather. In part, these results are expected because they merely support prior findings that defoliation by the western budworm varies inversely with precipitation (Hard and others 1980). But

these results also suggest that the relation between droughtiness and budworm survival could be represented by a dome-shaped curve, with reduced survival accompanying extreme drought.

Much of the observed relation between plant water (or nitrogen) and herbivore survival may not reflect a direct cause-and-effect relation (Clancy 1991). Rather, in all probability, the precipitation-survival correlation in WXBASE reflects underlying relations between available moisture and physiological responses by the host plants related to this moisture. Specifically, nitrogen "...can accumulate to higher than normal levels in the above-ground tissues of drought-stressed plants" (Mattson and Haack 1987). A relative shortage of foliar nitrogen has been postulated as a universal cause of massive mortality among young herbivorous insects (White 1974), and results from several studies suggest that western budworm survival is lower at both upper and lower extremes of foliar nitrogen (Brewer and others 1985, Cates and others 1987). In addition, Cates and others (1987) showed that "...terpenes interact with nitrogen in determining the quality of [budworm] food...," and "plant allelochemical concentrations appear to exhibit a dome-shaped relationship to drought stress" (Mattson and Haack 1987). Further, Scriber (1977) found that where leaf water of black cherry, *Prunus serotina* Ehrh., was limiting, larvae of *Hyalophora cecropia* (Linnaeus) were restricted in their ability to use ingested materials, including nitrogen. Finally, one group of investigators found lower survival in a pine sawfly, *Neodiprion autumnalis* (Smith), on severely moisture-stressed trees (McCullough and Wagner 1987), and another group found that leaf miners were more abundant on control trees than they were on the moisture-stressed ones (Bultman and Faeth 1987).

In summary, these results support Mattson and Haack's (1987) conclusion that "...severe and prolonged drought can become debilitating to phytophagous insects, just as it is to plants."

5.2.7 Environmental Modifiers

...we might define the environment in three different ways: as including only the elements perceived by the organism; as including all elements which affect the organism, whether perceived or not; or as including all elements that can be detected or inferred....We might call the first the perceptual environment...the second, the effective environment....The third, I suppose, is the total reality that worries the philosophical mind.
—From "The Forest and the Sea"
by Marston Bates (1960)

5.2.7.1 Statistically significant correlations—Western budworm survival rates were correlated with both several attributes of sites and stands and two indices of interstand influences. In evaluating these correlations, the following caveats apply. First, generally, only minor correlations were found between the budworm and these attributes. Second, these correlations were often inconsistent among areas. Third, within any given area, these correlations were commonly unstable across a range in budworm density.

Elevation, slope, and aspect—S_s was related to elevation, slope, and aspect (section 4.3.3.6). No doubt, these statistical correlations reflect an underlying cause-and-effect relation between temperature and budworm survival. Several projects also showed statistically significant relations between elevation and defoliation (section 4.4.3.6). These results suggest that budworm survival from fourth instar to pupae may be particularly low in the lower elevational portion of budworm host stands. Also, relations between elevation and S_A reflect a tendency for fecund moths to aggregate near the elevational

center of host stands (section 4.6.3.7). These results provide a partial explanation for findings by other investigators, who have shown that defoliation tends to be greatest across an elevational mid-range of their hosts (sections 4.3.3.6 and 4.6.3.7).

Site wetness—EG and site wetness varied together (section 4.2.2.5). Conversely, an inverse relation was found between S_L and site wetness (section 4.5.3.3). In sparse populations, this latter relation may reflect a higher average density of avian predators on the wetter sites. During outbreaks, it may reflect host tree responses to moisture stress in droughty situations (sections 4.2.2.5, 4.5.3.3, and 5.2.6).

Overstory composition—In IDA, defoliation and the proportion of true fir in the over-story increased together. And in both the Northwest (IDA) and the Southwest (NMEX), true fir sustained heavier defoliation than Douglas-fir. For Engelmann spruce, an appar-ent reversal was found between two regions: in IDA, defoliation and the proportion of spruce tended to increase together, but defoliation in NMEX was inversely related to spruce (section 4.4.3.7). In IDA, MONT, and NMEX, S_A and the proportion of Douglas-fir in the overstory increased together, but in both IDA and NMEX, S_A and the proportion of other host species in the stand varied inversely (section 4.6.3.8). Apparently, gravid females gravitate to stands with a high proportion of Douglas-fir foliage.

Crown depth—S_L and variation in crown depth increased together (section 4.5.3.4). These results support the idea that single-storied stands lose more insects through downward drift of the larger larvae.

Stand age—One area (MONT) exhibited a highly significant inverse relation between tree age and the number of egg masses found per emerging moth (S_A) (section 4.6.3.8). In three areas (IDA, MONT, and PNW), however, stand age and early survival (S_S) increased together (section 4.3.3.7). This latter relation suggests that host resistance to the budworm may decline as the trees reach and pass physiological maturity. Thus, the budworm-related problems commonly ascribed to old growth (for example, in Carlson and Wulf 1989) may arise primarily from a reduced ability of older trees to protect themselves against early instars.

Stocking—In NMEX, S_S was higher in fully stocked stands (section 4.3.3.7). This relation supports Mott's (1963a) premise that losses from early-instar dispersal increase in open-grown stands.

Shrub density—In IDA and NMEX, average defoliation was inversely related to shrub density. In MONT, however, the reverse relation was found (section 4.4.3.7). Practices designed to increase shrub density should only be applied in locations where moisture is not a principal limiting factor.

Interstand influences—One index, distance to the edge of visible defoliation (DST), was correlated primarily with S_S (section 4.3.3.5). This correlation undoubtedly arose primarily from short-range intertree and interstand dispersal of young windborne larvae. The second index, a measure of outbreak intensity (SIZ), was related to both S_S and S_A (section 4.6.3.6). The correlation between SIZ and S_S is compatible with the hypothesis that defoliation activates a defensive host-tree response. Although supporting evidence is missing, this correlation is also compatible with fragmentary evidence for some form of communication between attacked and nonattacked host plants (section 5.2.3.3).

5.2.7.2 Forest conditions and the western budworm—Many investigators believe that silvicultural treatments provide a viable way to mitigate adverse effects of the western budworm (Anderson and others 1987, Carlson and Wulf 1989, Langelier and Garton 1986, Schmidt and others 1983, USDA 1986). In fact, this retrospective study arose largely because I share that belief. Unfortunately, the results of this study show conclusively that, compared with prior budworm density and year effects, only minor statistically significant relations were found between the budworm and other environmental attributes (table 27); in every study area, relations between environmental attributes and the budworm were unstable across a broad range in budworm density; and even within any given density range, these relations were inconsistent among areas (sections 4.2.2.2, 4.3.3.2, 4.4.3.2, and 4.6.3.2).

Undoubtedly, many factors complicate relations between environmental attributes and budworm numbers. Four such factors are discussed below.

First, autocorrelations among many of the site and stand indices (for example, stand age and variation in crown depth) can frustrate attempts to derive meaningful correlations between these indices and changes in budworm numbers, or to interpret the correlations that are derived.

Second, current density provides a convenient surrogate for the net influence of both the external environment and prior density. By extension, autocorrelations between environmental attributes and current density tend to mask relations between these same attributes and future density. Undoubtedly, such autocorrelations have resulted in some of the high correlations in hazard-rating schemes, such as those of Stoszek and Mika (1985), which do not use current density when correlating environmental attributes with future density or defoliation.

Third, except when budworm populations are sparse and numerically stable, the dynamics of a population may be dominated by mass flights of gravid moths. Because such flights can occur on a massive spatial scale, both large-area phenomena and on-site conditions can be important. At present, this mix of processes gives these mass flights a huge stochastic component.

Fourth, most of what we know about relations between the forest and the western budworm has been derived from outbreaks. For reasons described later (section 5.3.1.3), such knowledge cannot yield consistently reliable guidelines for silvicultural treatments to prevent future outbreaks. And even during outbreaks, much of the inconsistency between the environmental indices I used and the numerical behavior of the budworm may merely reflect a poor matchup between some of these indices and processes that are important in budworm dynamics.

Significantly, most of the environmental indices I used are based on the indices Wulf and Carlson (1985) used to develop their indexing model for budworm-susceptible stands. Further, my regression models follow the multiplicative form Wulf and Carlson used in their model. Thus, the redundancies, shortcomings, and inconsistencies revealed in the indices used here are necessarily also present in Wulf and Carlson's model. The results shown here clearly do not support either Wulf's (1985) assertion that the indexing model provides a "...holistic picture of budworm habitat quality" or the description of that indexing model by Carlson and others (1985a) as "...a strong working hypotheses for...budworm dynamics." In any case, more useful relations will undoubtedly be found between environ-

mental attributes and the budworm as we learn more about important underlying processes, and formulate more appropriate indices.

5.2.8
Population Modes
and Phases

...if the environment changes to relieve the population of pressure from a previously sovereign effect, the population will increase until it reaches a second equilibrium level where another effect halts it.
—From "Sociobiology: the New Synthesis"
by E.O. Wilson (1975)

Stipe (1987) used defoliation trends, forest type, and climate to identify 16 "zones of infestation" for the western budworm. Across these zones, area of host type totaled about 60 000 000 ha. Throughout this range, detectable western budworm populations appear to persist indefinitely in host stands.

Where foliage sampling has been conducted, western budworm egg densities have ranged across about five orders of magnitude (from about 0.1 to 12,000 eggs per m²). Both catches of adult moths at pheromone-baited traps and a few direct foliage samples (fig. 49) suggest that persistent populations exist at still lower densities.

Anderson and others (1987) used tree-ring-width chronologies to reconstruct the duration and intensity of past budworm outbreaks in western Montana. They concluded that three outbreaks occurred in the sampled areas between 1814 and 1910 (before fire suppression), and two in the 70 years since. Outbreak duration averaged 13.3 years before 1910, and 25.4 years since then. Similarly, Swetnam and Lynch (1989) used tree-ring-width chronologies to reconstruct the timing, duration, and radial growth impacts of past outbreaks in portions of Colorado and New Mexico. They concluded that:

> At least nine outbreaks were identified...from 1700 to 1983. Severity and timing of outbreaks was highly variable. The average duration of reduced growth...was 12.9 years and ranged from 5 to 26 years. The average interval between...outbreaks was 34.9 years and ranged from 14 to 58 years....Since [the mid-20th century] outbreaks have been markedly more synchronous among the sampled stands.

Even in the northern Rocky Mountains, where an outbreak has now persisted since about 1948 (Fellin and others 1983, fig. 57), the budworm outbreaks that occurred earlier in this century usually declined within a few years. Specifically, information on "infestations...reported annually from National Forest Ranger Districts in the Northern Region...1922 through 1953" (Johnson and Denton 1975) shows that 91 budworm outbreaks were reported in this Region during this period. Of these, 44 (48 percent) persisted for only 1 or 2 years (fig. 55, p. 119).

Tree-ring chronologies may fail to record minor outbreaks, and aerial sketch mapping covers only a few decades. Nevertheless, the apparent aperiodicity of outbreaks in the tree-ring-width chronologies, the indeterminate duration of outbreaks, and the results of direct foliage sampling all suggest that populations of the western budworm are usually either barely discernible by standard sampling techniques, or at densities so high that defoliation is obvious. In other words, the western budworm has a dual equilibrium life system, similar to that proposed for the eastern budworm in Morris (1963d), as well as various other species (sec. 5.2.2.5). As noted in Campbell (1987), "...this pattern...focuses attention on the two major population modes (outbreak and sparse) and the two transient
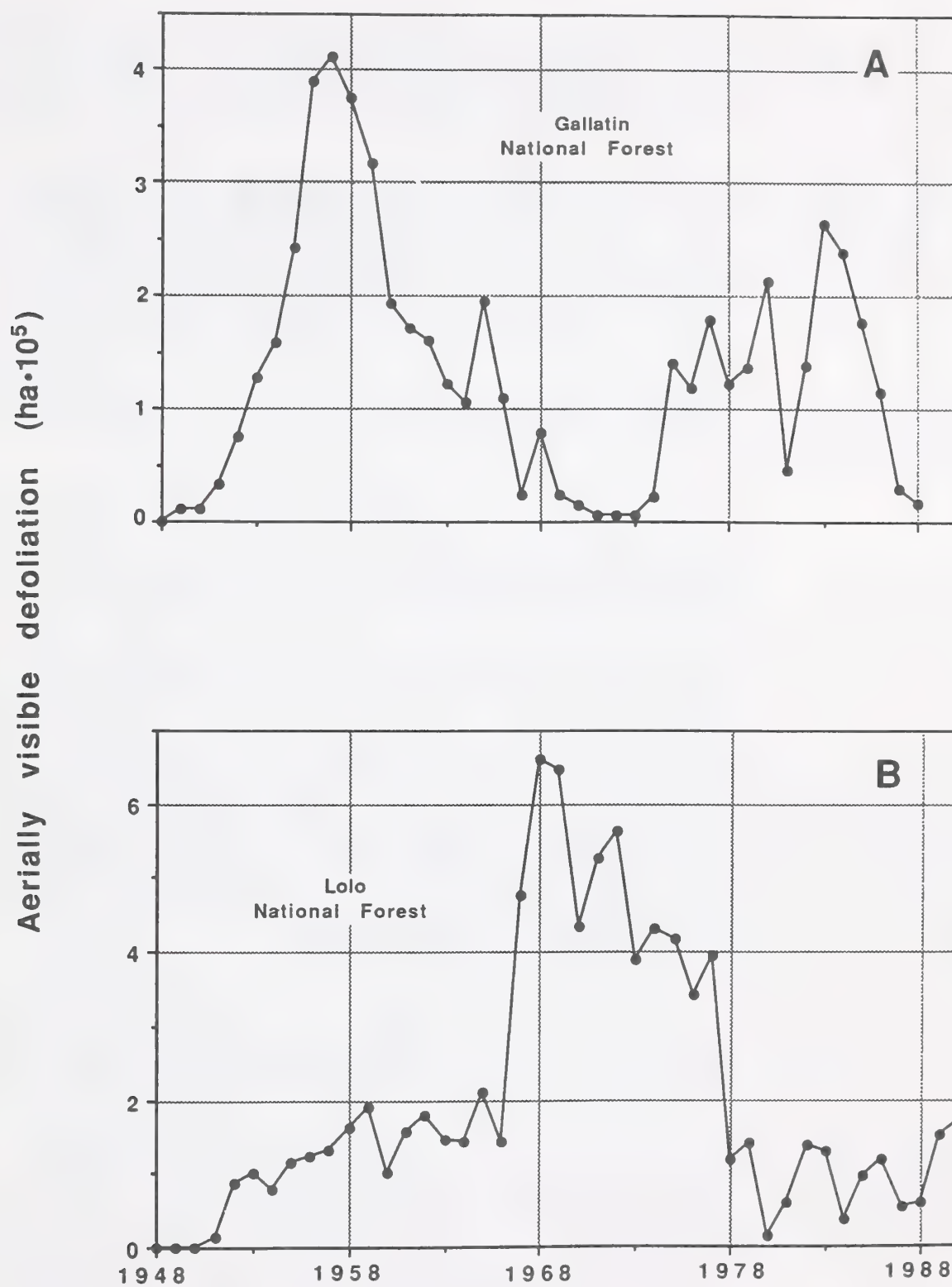
Figure 57—Defoliation trend on the Gallatin and Lolo National Forests, Montana (1958-84) (data provided by L.E. Stipe).

phases (release and decline) where we must have information...."

5.2.8.1 Release phase—Recently, Wulf and Cates (1987) concluded as follows:

> ...stand conditions represent the underlying cause of outbreaks because...the effects of weather and natural enemies...are mediated by the quantity and quality of available food....Outbreaks arise...whenever and wherever the quantity and quality of the food resource is sufficient to impart [an]...increase in...survival...that cannot be compensated for by mortality from natural enemies."

In fact, projections from the simulator suggest that western budworm outbreaks rarely arise in place. When site, stand, and weather indices were set at their approximate mean values, N_E stabilized at about 13 eggs per m². Even when simulated site, stand, and weather conditions were optimal for survival, N_E again stabilized at about 42 eggs per m².

When a nearby outbreak was simulated, S_S began to increase; presumably, the increase resulted from dispersing wind-borne larvae. With S_S higher than before, S_L began to increase as a consequence of the inverse relation between N_L and S_L across fourth-instar densities between about 1 and 50 per m². Also, the ratio between N_M and preceding N_A began to increase as the model simulated inflights by fecund moths. In addition to the above processes, the results in equation (50) indicate that egg-mass deposition in an incipient outbreak may tend to increase during subsequent seasons as the moths respond positively to the presence of recent defoliation or other budworm activity.

5.2.8.2 Outbreak mode—In the northern Rocky Mountains, a massive but rather low-intensity outbreak (Fellin and others 1983) has persisted for four decades. In other areas, such as the Blue Mountains of eastern Oregon, the outbreaks that have been documented have persisted for less than a decade. Defoliation during the most recent (1980s) outbreak in the Blue Mountains has been particularly severe, however.

During massive outbreaks, local declines in generation survival are likely to be offset by inflights of gravid moths from more dense, windward populations. Because of their strong density-dependent component, such flights tend to ensure that even marginally susceptible stands will participate in the outbreak. In prolonged outbreaks, however, circumstantial support has been found for Perry and Pitman's (1983) contention that infested stands are producing foliage toxic to many of the young larvae as they seek to establish themselves in new buds and needles. Whatever the cause, the strongly density-dependent survival rate among these larvae is simply too low to produce enough subsequent larvae to strip the current-year foliage.

In an evolutionary sense, the above phenomena appear to accommodate both the budworm and host trees reasonably well. By defending themselves, the host trees minimize budworm survival before the insect has reached a stage where it would otherwise be able to strip all of the new foliage and ultimately kill the trees. Through low values of S_S, the budworm population is prevented from exhausting its food base, and the population can achieve a high-density quasi-equilibrium. Stated another way, these phenomena appear to represent a stabilizing negative feedback process (Odum 1969). Unfortunately, although the process allows the stand to maintain site occupancy, much of its annual production is immediately converted into budworm biomass. Apparently, mass outflights not only relieve pressure on defoliated stands, but also help to ensure that exploitable stands will be found and that the population will persist.

5.2.8.3 Decline phase—Both the OREG data and the historical record suggest that the current outbreak in eastern Oregon will soon collapse. Since 1985, both S_S and S_L have been systematically declining in OREG. Consequently, average survival from eggs to adults (S_G) has declined about 10-fold. For example, starting from 300 eggs per m², the simulator projects average S_G at about 0.0225, under conditions similar to those found in OREG before 1986. By 1988, this average had fallen to only about 0.0022.

In the life systems of both the western and eastern budworms, population declines over millions of hectares could sometimes occur when major population declines in highly sus-

ceptible stands stop inundations of more marginal stands by inflying gravid moths. Green-bank (1957), for example, noted that dense eastern budworm populations "...in young, open, or mixed-wood stands...soon decline unless bolstered by repeated invasions."

In the absence of adverse weather, populations similar to those in WXBASE should stabilize (I_M = 1) at about 15 egg masses per m² (fig. 58). If a sufficiently widespread weather pattern during May brings cool, wet weather, however, an outbreak is likely to collapse. Cool, wet spring weather for two consecutive years would greatly reinforce the effect of a single season. Budworm outbreaks should also decline after exceptional cold in January or unseasonable warmth in March.

Through their aggregative abilities, generalist natural enemies may cause many incipient budworm outbreaks to collapse (section 5.2.1.4). Other conditions that are unlikely to sustain a prolonged outbreak include sites that are wetter than average and stands that include a major spruce component.

5.2.8.4 Sparse mode—Clearly, the combined effects of predaceous birds and ants provide a lower stable equilibrium density for populations of the western budworm, at least in northwestern forests. Indices of conditions where low budworm densities are likely to be maintained include wetter than average sites, a low proportion of Douglas-fir foliage in the overstory, and low variation in crown depth.

5.2.8.5 Population equilibria in the eastern budworm—Royama (1984) rejected the dual equilibrium theory of Morris (1963d). First, Royama argues that the data "...show no clear sign of an endemic equilibrium...." Second, he notes both that survival at innocuous densities does not respond positively to "favorable" weather, and that food shortage "...is not a universal cause of population decline." Third, Royama argues that Watt's (1963) curve, which shows increasing survival with increasing density, "...does not imply a causal effect of density on survival and, therefore, is irrelevant to the question of shape in Morris's reproduction curve." Royama concludes:

> ...there is no reason to assume the dichotomy of endemic and epidemic state...My hypothesis...with only one equilibrium point is consistent with the evidence....

Regarding Royama's first point (no low-density equilibrium), I suggest that a run of 10 consecutive years at or below one larva per m² (Royama 1984) constitutes powerful evidence that something was maintaining this population at low densities. Further, results summarized from Miller and Renault (1981) (section 4.7.3.2) show conclusively that this "something" could not possibly be induced by Royama's "fifth agent." Rather, the evidence points to predation.

Second, Royama dismisses both favorable weather as a probable cause of budworm outbreaks and food shortage as a "universal" cause of decline. For both budworm species, the latter point, at least, appears to be valid. Neither point, however, is crucial to the question of whether the numerical behavior of the population is bimodal.

Third, Royama dismisses Watt's (1963) curve because it does not imply a causal effect of density on survival. For both the eastern and western budworms, however, a clear cause-effect relation has been demonstrated between density and predation (fig. 54).
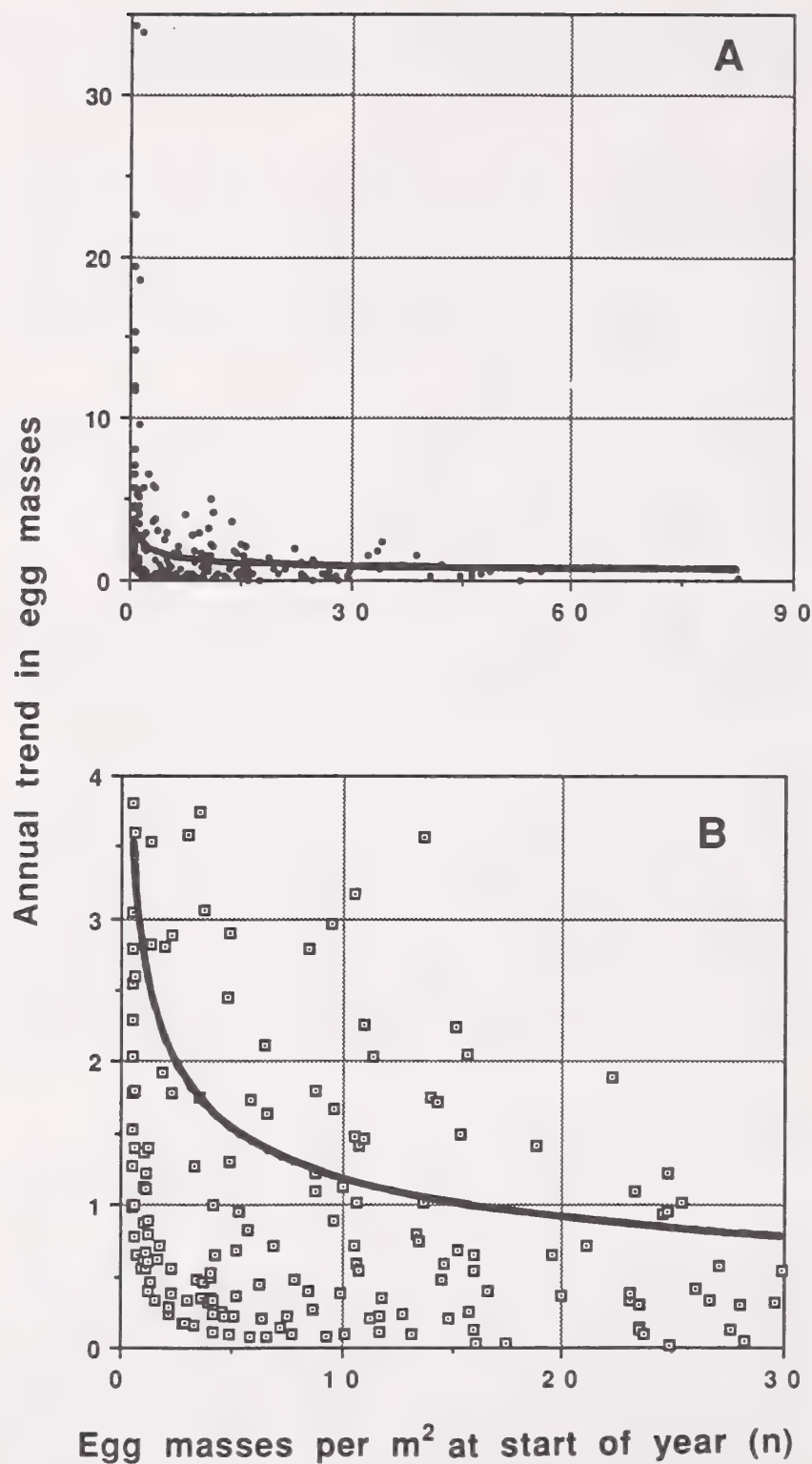
Figure 58—Egg-mass trend ($N_{M(n+1)} / N_{M(n)}$) in WXBASE: A, all observations; B, detail, showing principal relation between egg-mass density and subsequent trend in that density.

Finally, in arguing for a life system with one equilibrium point, Royama assumes "...that the intensities of factors affecting regional budworm population dynamics have been repeating the same temporal pattern over and over" (Fleming 1985). As Blais (1985) notes,

> ...it is difficult to accept this theory considering some shorter intervals between outbreaks during the 20th century and especially much longer ones prior to this century.

Specifically, Blais (1965) concluded that

> ...the intervals between the last six budworm outbreaks in the Laurentide Park in Quebec Province are 44, 60, 26, 76, and 37 years, respectively. These irregular intervals indicate that occurrence of any future outbreaks cannot be predicted with any accuracy on the basis of periodicity of past outbreaks.

Western budworm populations have also shown no tendency to regular, cyclic behavior.

Berryman and others (1987) suggest that cyclic outbreaks result "...from long time-delays... in...regulatory feedback loops...." Accumulation of overstory biomass and advancing age of the stand after an outbreak could provide such a time-delay process in forests susceptible to the eastern budworm (Holling and others 1976). Berryman (1987) classified both the western and eastern budworms as eruptive pests, and Berryman and others (1987) note that irregular outbreaks may occur "following [pest] immigration...or a disturbance caused by density-independent factors." Clearly, either of these latter processes could trigger an outbreak of either the eastern or the western budworm. In any event, the evidence thus far assembled is consistent with dual equilibria for both species.

5.2.9 Sampling in Population Studies

...refuse to be hypnotized by the elegance of modern sampling design....Sampling has no intrinsic merit but is only a tool which the entomologist should use to obtain certain information provided there is no easier way to get the information....
—From "Annual Review of Entomology"
R.F. Morris (1960)

5.2.9.1 Precision—Estimates of budworm densities form the basis for most budworm-related field research; they are essential for making pest-management decisions and evaluating control tactics. Optimal sampling methods provide these estimates with acceptable precision while minimizing costs.

In any given study, the precision that is acceptable should be defined by the intended uses of the sample data. Nevertheless, as noted by Southwood (1978):

> ...the law of diminishing returns applies as one attempts to reduce the statistical errors of sampling and in the long run, more knowledge of the ecology of the animal may be gained by studying other areas or making other estimates or even by just taking further samples than by straining for a very high level of accuracy in each operation.

For damage assessment and control studies on numerically volatile insect pests, Southwood suggests "...an estimate of population density with a standard error of about 25% of the mean...." For life-table studies, he notes that "...the level is frequently set at 10%." Because a precision of 15 percent can be achieved with less than half the samples needed to achieve 10 percent, however, investigators may be unrealistic to specify that sampling should continue after 15 percent precision has been attained, unless the budworm populations to be sampled are very dense. Similarly, Mason (1989) advises investigators to keep monitoring schemes as simple as possible "to ensure perpetuity [of the sample estimates] during periods of austerity."

5.2.9.2 Studies on population dynamics—During preliminary analyses of eastern budworm survival in New Brunswick, MacDonald (1963b) decided to discard a portion of the data because these data described "inordinately high survival" among late instars. As MacDonald explained: "As only mid-crown branches were sampled, this [apparent survival] was probably caused by a downward movement of large larvae following defoliation of the upper crown." More generally, it is common knowledge that budworm densities differ among parts of their forest universe (Carolin and Coulter 1972, 1975; Harris 1963, 1977; Morris 1955; Schmid and Farrar 1982).

Multicrown sampling (Morris 1955) provides an obvious way to deal with the problem encountered by MacDonald. Unfortunately, although accurate estimates of average whole-plot densities are crucial for the successful conduct of studies on budworm population dynamics, the cost of extensive multicrown sampling to derive these estimates usually has been beyond the means of prospective investigators.

Data acquired to date on western budworm populations have not revealed a problem similar to that encountered by MacDonald (1963b). Undoubtedly, the same problem occurs in both species in places where the later instars exhaust current-year foliage before they have completed larval development. Fortunately, however, strongly density-dependent values of S_s in the western budworm (sections 4.3.3.1, 5.2.3) usually ensure that N_L will remain below a threshold where this overcrowding phenomenon occurs. In short, in places where intrastand patterns of western budworm occurrence are similar to those described in Campbell and others (1984a), investigators can derive reliable estimates of average whole-plot densities by sampling from midcrown tips until the desired precision is reached. By using either locally derived estimates of intrastand foliage distribution or published estimates, such as those in Carolin and Coulter (1972), Mason (1970), or Srivastava and others (1984), they can then weight the contribution of each crown third and tree height class to derive estimates for whole plots. In particular, the many similarities in density-survival relations among the three budworm species (figs. 45-46, 48, 50-51) provide strong support for the idea that samples drawn from midcrown tips, together with information on intrastand patterns of budworm occurrence (Campbell and others 1984a), can provide an acceptably precise sequence of density estimates for many studies on the population dynamics of the western budworm.

5.2.10 Density Dependence and Population Dynamics

An astonishing diversity of biological responses have been identified as density-dependent controls. Most of them are implicated in one way or another in social behavior and, indeed, much social behavior is comprehensible only by reference to the role it plays in population control.

—From "Sociobiology: the New Synthesis" by E.O. Wilson (1975)

5.2.10.1 Host responses to herbivory—The dynamics of western budworm populations appear to be determined largely by the following density-related processes: (a) density-dependent relations between the budworm and its natural enemies when populations are sparse, but inverse density-dependent relations between the pest and these enemies when the budworm is increasing to outbreaks (section 5.2.1); (b) density-dependent endogenous (intrinsic) relations that influence mass moth outflights and inflights (section 5.2.2); and (c) density-dependent herbivore-host relations that are triggered by significant defoliation (section 5.2.3).

The density-related nature of both predator-prey relations and endogenous population processes is a widely recognized principle of population ecology (Huffaker 1971, Price 1984, Solomon 1969), and a coevolutionary process of attack and counterattack among plants and herbivores is broadly recognized (Ehrlich and Raven 1964, Odum 1971, Price 1984). Surprisingly, however, I have found less than universal recognition that host responses to herbivory are also necessarily density dependent. For example, conclusions reached by Wulf and Cates (1987) about the dominant role of foliage quality in western budworm population dynamics do not appear to have been tempered by considerations of density dependence in this process (section 5.2.8.1).

I believe that broad recognition of host responses to herbivory as a density-related phenomenon is bound to lead to a better understanding of herbivore population dynamics as well as effective strategies and tactics for pest management.

5.2.10.2 Critical age-intervals—In any life system, relations between density and survival may differ dramatically among the age-interval components of a single generation. In populations of the western budworm, for example, inverse relations between pairs of age-interval survival rates clearly reflect major density-stabilizing influences (section 4.1.5). Unfortunately, the opportunities and constraints implied by such intragenerational relations are not always recognized. For example, most attempts to evaluate the role of biochemical variation in host foliage in western budworm survival have concentrated on current-year foliage and late instars (Cates and Redak 1988). Such attempts are bound to be disappointing if the principal density-dependent mortality occurs when second instars emerge from hibernation and attempt to mine old needles (section 5.2.3.1).

In another example, Elkinton and others (1989), who summarized recent studies on sparse gypsy moth populations, based their conclusions largely on the results of a study of predation on gypsy moth pupae. From this study, they concluded that "...small mammal predation on low density populations ... may be essentially indistinguishable from density independent predation." Because these authors found extremely high pupal mortality from small mammals in sparse populations, they suggested that:

> We think it is entirely possible that low density gypsy moth populations may not be regulated at all...but fluctuate asynchronously which, coupled with dispersal, leads to *apparent* stability on a regional scale.

In fact, for at least half a century, the gypsy moth persisted at generally innocuous densities in the predominantly oak forest of northeastern Connecticut and adjacent Massachusetts (Campbell and Sloan 1977). Life-table studies that were conducted on these sparse and numerically stable populations between 1965 and 1971 revealed that populations below about 1,000 eggs per acre (about 2,400 eggs/ha) tended to increase from one year to the next, but those above this density tended to decrease. Further, this relation was close—on a logarithmic scale, $R^2 = 0.714$ (N = 28) (Campbell and Sloan 1978). In short, these results reflect a sparse, numerically stable gypsy moth population system in which annual trend depends on density. The same data revealed that most of this year-to-year density dependence was associated with density-dependent variation in survival among the large larvae. Specifically, survival among these larvae declined "...from about 28% starting with 100 eggs per acre to about 1% starting with 100,000." Conversely, pupal survival among these populations "...was relatively invariant...[but] averaged only about 18%" (Campbell 1976).

These results show that the crucial density-dependent process or processes in sparse and numerically stable gypsy moth populations must occur primarily during the large-larval interval. Thus, no amount of work on mortality-causing processes that are occurring during another interval, such as the study on gypsy moth pupae summarized in Elkinton and others (1989), is likely to reveal the density-dependent attribute or attributes that sometimes retain gypsy moth populations at low densities.

5.2.10.3 Key factors and cycles—For many species, Morris (1957) thought that population studies would ultimately reveal a few "key factors" that are mainly responsible for population changes. And although few truly numerically cyclic species have been described and studied, it is not surprising that the cyclic behavior of these species often appears to be derived from a single dominant process; for example, see Baltensweiler and Fischlin (1988), Baltensweiler and others (1977), Haukioja (1980), Pitelka (1959, 1964), and Schultz (1964). Significantly, each of the species described by these particular studies appears to alternately induce changes in host foliage quality (through defoliation) and then respond to this altered food quality (through population decline).

In the numerically bimodal populations of the western budworm, four more or less distinct subsets of key factors have been identified. First, natural enemies operate to keep the population sparse (section 5.2.8.4). Second, many new outbreaks may be triggered by migrants (section 5.2.8.1). Third, low-intensity outbreaks may be maintained largely by defensive host stand responses to defoliation, coupled with continued redistribution of the budworm through moth dispersal (section 5.2.8.2). Fourth, even under chronic outbreak conditions, adverse weather coupled with changes in host foliage and a reduction in gravid inflying moths may result in outbreak collapse (section 5.2.8.3).

Significantly, no key factor appears in all four of the above subsets, although both budworm dispersal and host responses to defoliation are common elements in several subsets—three for dispersal and two for host responses.

I hope future investigators will carefully consider patterns in numerical behavior in their attempts to evaluate the possible role of any given process in the population system of the species being studied. For example, the roles suggested for pathogens in forest insect population dynamics by Anderson and May (1980) and for host responses to defoliation in herbivore population dynamics by Schultz and Baldwin (1982) are both based on the assumption that the herbivore's behavior is numerically cyclic. Unfortunately, however, at least one species these authors used to illustrate their theses (the gypsy moth) is known to exhibit a numerically bimodal pattern, at least in North America (Campbell and Sloan 1978, Elkinton and Liebhold 1990), similar in many respects to that of the western budworm. As Peterman and others (1979) noted "...understanding and management schemes often fail, in part, because we are viewing the system with the wrong conceptual framework."

5.2.10.4 Modeling density dependence—Murray (1979) maintains that density dependence is merely a hypothesis and, in fact, no evidence of density dependence has been detected in some field studies, at least by the original investigators (Andrewartha and Birch 1954, Dempster 1983, Elkinton and others 1989, Stiling 1988). In several such instances, conclusions reached originally about the sporadic nature or nonoccurrence of density dependence have subsequently been disputed (Hassell and others 1989, Smith 1961, sec. 5.2.10.2). Originally, for example, Stiling (1988) analyzed 63 life-table studies of 58 insects species and concluded that more than 45 percent of the studies "...reveal

a complete absence of conventional density dependent mortality." Subsequently, though, Hassell and others (1989) showed that "...the proportion of [these] studies in which density dependence was detected by the original authors increases markedly with the number of generations [examined]." In any case, such negative findings have led to the notion that density-dependence merely sets an approximate "floor and ceiling," leaving stochastic processes to drive the population in between (Milne 1957, Stiling 1988, Strong 1986).

A clear understanding of how naturally occurring population control mechanisms work is of fundamental importance in our efforts to solve problems such as controlling insect pests, setting harvest limits, and conserving endangered species. To take one example, if we assume that the population fluctuations of the Bay checkerspot butterfly, *Euphydryas editha* Boisduval, are density independent, then the simulated threat to extinction of this insect posed by such disturbances as sampling is markedly greater than if we assume that its population fluctuations are density dependent (Harrison and others 1991). Which assumption is more realistic?

Foliage-eating pests—In their concluding remarks, Hassell and others (1989) noted that "...we see little need, at least for insects, to cast aside the familiar notion of populations persisting by virtue of density-dependent processes operating over a broad range of population densities."

Certainly, that recommendation is supported by both the findings reported here for three North American budworms and the broader literature on the population dynamics of foliage-eating forest pests.

Density-related processes in the life systems of foliage-eating pests commonly include functional and numerical responses by natural enemies; behavioral and physiological responses by the herbivore, such as those that optimize survival, increase dispersal, or limit fecundity; defensive responses to defoliation by the host plants; and mass starvation of the pest herbivore. Further, a shift in the effect of many of those processes can be associated with some approximate threshold density of the herbivores. (Several of these processes, in fact, are defined by the presence of such a threshold.) Also, in any given herbivore life system, these thresholds differ widely among the various density-related processes. Thus, rather than a "floor and ceiling" model, it might be useful to think of density dependence as a density-response stairway with many steps—at least in pestlike life systems.

Undoubtedly, density-related processes interact with each other, as well as with many other environmental components, often in ways that can only be unraveled by studies that go far beyond the resources of most population ecologists. For example, concerning the major needle-eating budworms and the gypsy moth, a spatial definition of "population" that yields biologically meaningful information at an innocuous density may be limiting or even misleading during an outbreak (section 5.2.2.5). In consequence, the blurred and (often) approximately linear relations we find within a sequence of herbivore densities and describe as "density dependence" are merely the net visible outcome of a complex network of interacting processes. Despite this complexity, I agree with Morris (1957) that the dynamics of many forest defoliators are probably dominated by a few principal processes. Once these key processes have been identified, building a useful population model should become a manageable task. Without such information, however, our attempts to build such a model are likely to end in failure.

Foliage-eating nonpests—Earlier (section 5.2.1), I concluded that predaceous birds and ants begin a noticeable response to budworm density above a threshold near 0.1 half-grown larva per m² of foliage. To my knowledge, no density-related process has been identified that systematically depresses budworm survival when budworm densities are in a range below this threshold. Significantly, although the budworms are among the leaf-eating forms preferred as food by many generalist natural enemies (section 5.2.2.5), many of the lepidopterous associates of the budworms appear to fluctuate around mean values lower than this threshold.

Wilson (1975) has likened a density-independent population to a gambler playing against an infinitely powerful opponent. Accordingly, sustained density-independent population fluctuations inevitably lead to extinction, as others have noted or implied (Harrison and others 1991, Hassell and others 1989). That this dangerous life strategy is itself a rarity is virtually guaranteed by the existence of a huge array of nonpest herbivores. As Morris (1963d) noted, "...reproduction curves for the great majority of forest insects...[exhibit] a continually decreasing slope [with increasing density]...." I believe, therefore, that population fluctuations in foliage-eating nonpest insects are usually weakly density dependent, with their upper boundary usually set by functional responses of generalist natural enemies. Although direct evidence is woefully fragmentary, I suspect that the density dependence in herbivore life systems at low herbivore densities is usually induced primarily by a combination of weak functional responses and small-scale aggregative responses by natural enemies.

5.2.10.5 What limits herbivore numbers?—As part of a general theory of population control, Hairston and others (1960) concluded that, "Herbivores are seldom food-limited, appear most often to be predator-limited, and therefore are not likely to compete for common resources." Subsequently, in response to critiques of their original paper by Murdoch (1966) and Ehrlich and Birch (1967), these authors qualified some of their original conclusions, specifying that "...we are not making statements about most herbivores...our statements...apply to the quantitatively dominant species...." (Slobodkin and others 1967).

In contrast, Ehrlich and Birch (1967) proposed that a realistic basis for dealing with changes in population numbers should include the following propositions:

- All populations are constantly changing in size.
- The environments of all organisms are constantly changing.
- Local populations must be recognized and investigated if changes in population size are to be understood.
- The influence on population size of various components of the environment varies with population density, among species, among local populations, and through time.

Slobodkin and others (1967) noted that their conclusions about predator limitations in herbivores "...can be falsified if none of the herbivores capable of damaging the dominant vegetation is predator limited." Clearly, all of the conifer-eating budworms discussed here are limited by processes that operate through three different trophic levels [producer (section 5.2.3), herbivore (section 5.2.2), and secondary consumer (section 5.2.1)]. For this group of herbivores, the propositions of Ehrlich and Birch (1967) are far more useful than the theory of Hairston and others (1960). Ironically, in qualifying their original thesis, Slobodkin and others (1967) explicitly restricted their notion to the group of herbivores that appear least likely to be limited primarily by natural enemies—at least with respect to the processes that limit populations of foliage-eating forest insects.

**5.3
Management
Considerations**

*The ordinary citizen today assumes that science knows what makes
the community clock tick; the scientist is equally sure that he does
not.*

—From "A Sand County Almanac"
by Aldo Leopold (1949)

**5.3.1
Rating Stand Hazard**

*...previous experience...may keep one from seeing things as they
really are.*

—From "Quaestiones entomologicae"
W.G. Wellington (1965b)

The hazard posed to interior mixed conifer stands by the western budworm includes both
the likelihood that an outbreak will occur (susceptibility) and the damage that is likely to
result from such an outbreak (vulnerability). Factors that influence stand susceptibility
and vulnerability once an outbreak occurs are summarized below.

5.3.1.1 Susceptibility to outbreaks—Mott (1963b) defined the susceptibility of a forest
stand to outbreaks of eastern budworm to include "...both the intrinsic factors that affect
the survival rate of resident populations and the extrinsic factors ...that affect the dispersal
of air-borne populations into or out of the stand."

For defining stand susceptibility to western budworm outbreaks, influences equivalent to
Mott's "intrinsic factors" are summarized here under the heading "on-site factors." Mott's
"extrinsic factors" are summarized under "interstand influences." I have added two more
categories. The third category, "outbreak history," includes indices of changes in foliage
quality that were induced during a prior outbreak or outbreaks. The fourth category,
"weather," includes weather regimes that favor budworm survival.

On-site factors—Wulf and Cates (1987) state that "Susceptibility and vulnerability are
both recognized as related to the same site and stand characteristics." Starting from this
assertion, Wulf (1985) assumes that relations between forest conditions and the bud-
worm that were derived primarily during outbreaks can be extrapolated to innocuous
populations to conceptualize "...a model that will index stand susceptibility across the
full range of forest conditions associated with western spruce budworm." Unfortunately,
I have been unable to show that most of the site and stand attributes specified in Wulf
and Cates' 1987 paper as indices of susceptibility are reliable indices of processes that
play roles in the dynamics of resident sparse populations (sections 4.3.2.6, 4.5.1.1,
4.6.2.6, and 5.2.7).

Active interstand redistribution of eggs by fecund moths, passive wind-borne redistribution
of small larvae, or a combination of both processes are sometimes sufficient to obliterate
the depressant effects of on-site processes that would otherwise maintain resident popula-
tions at innocuous densities (sections 4.3 and 4.6). In the absence of significant interstand
redistribution, however, innocuous densities appear to be maintained primarily by an
inverse relation between N_L and the mortality rate of large larvae and early pupae from
predation (sections 4.5.2, 5.2.1.2). During these relatively sedentary stages, processes
that particularly favor high survival are related to both relatively dry sites and stands with
high variation in crown depth. On-site factors that favor S_s do not appear to be greatly
influenced by stand conditions, except for increasing stand age, but this rate does vary
in response to indices of site temperature (elevation, slope, and aspect).

Later, during interstand flight, the moths appear to be attracted to stands with a high component of Douglas-fir (fig. 40). Conversely, moths may tend to avoid stands with a high Engelmann spruce component, at least in the Southwest (fig. 42).

Interstand influences—Although long-range larval dispersal may occasionally be significant, as postulated by Carlson and McCarthy (1989), detailed studies on larval dispersal of both the Douglas-fir tussock moth (Mitchell 1979) and gypsy moth (Mason and McManus 1980) show that most of the dispersing larvae of these forest defoliators will be deposited within a kilometer of their point of origin. Similarly, the results presented here (section 4.3.3.5) suggest that western budworm larval dispersal is a relatively short-range phenomenon, with its principal influence on the sparse populations to which these larvae may migrate. For most stands, the practical consequences of larval dispersal appear to be spatially constrained to a radius of a few kilometers from their source.

Unlike the passive dispersal of larvae, active interstand dispersal of eggs by gravid moths appears to have major consequences across distances much greater than 10 kilometers. I believe that adult dispersal is the attribute of the budworm life system that poses the greatest challenge to managers who must deal with the budworm problem in western forests. Managers should consider the following spatial relations in rating the hazard that stands will be invaded by fecund moths:

- In general, long-range invasions can be expected when upwind forests are supporting dense budworm populations.

- Moth invasions may be particularly likely during years when upwind forests have been severely defoliated for the past 2 or 3 years in succession (section 4.6). As noted by Raske and Sutton (1985), stand vulnerability (to eastern budworm) depends in part on the susceptibility and vulnerability of the forest upwind.

- As previously noted, Greenbank and others (1980) found that the average duration of relatively short flights was about 35 minutes and that the landing of moths was directly related to the presence of host trees. Together, these findings suggest that downwind forests may be particularly susceptible to massive moth invasions when they are bounded on their upwind side by fairly wide expanses of nonforested land. Both the New Mexico Suppression Project and the Montana B.t. Project are in just such locations—and both areas have a long history of budworm outbreaks.

Outbreak history—Under most nonoutbreak conditions, variation in host foliage quality probably plays no role in determining stand susceptibility or resistance to the initial outbreak (section 5.2.3). Patterns of budworm survival across the course of an outbreak, however, strongly suggest that host responses to defoliation result in increasing resistance (sections 4.3, 4.4, and 4.5).

Although direct evidence is lacking on the time required for defoliated trees to regrow foliage, some results suggest that increases in resistance may not disappear for several years after an outbreak has ended. For example, Baltensweiler and Fischlin (1988) report that once larch trees have been defoliated by the larch budmoth, 2 to 7 years may be required for the needles to recover their average quality. Thus, stand susceptibility to a new outbreak may be particularly low in the first few years after the termination of a multiyear outbreak episode.

Weather—Results reported here suggest that budworm survival will be particularly high during years characterized by cooler than average weather during March, a dry period during larval dispersal in May, and a relatively, but not excessively dry period during May, June, and July. Particularly during a sequence of two or more such years, generation survival in innocuous populations may be sufficient to exceed low-density thresholds and initiate an outbreak.

5.3.1.2 Vulnerability to damage—In Brookes and others (1985), **damage** is defined as "any effect of insect feeding deemed deleterious to some management objective or objectives." To at least one economist (Bible 1985), "...budworm damage [in general] consists of tree mortality and growth losses during and after an outbreak." Others include less quantifiable impacts under "damage," such as "...those associated with aesthetic quality, recreation, hydrology, wildlife, and fire hazard." (USDA 1986). However defined, all these impacts are linked to the budworm through cumulative defoliation. For that reason, the focus of this section is on both the factors that maintain outbreaks through time and those that influence defoliation intensity during those outbreak years.

On-site factors—During outbreaks, western budworm survival from eggs to fourth instar was much higher in westerly study populations than in those farther east (fig. 45, section 5.2.3.4). Following this pattern, stand vulnerability to a given outbreak should be highest in stands that are farther west. Thus, although western budworm outbreaks have been less common in westerly forests (Kemp 1985, Kemp and others 1985), outbreaks that do occur in the westerly area can be expected to have relatively severe economic consequences.

Under outbreak conditions in any given area, most of the variation in each dependent variable (EG, N_L, DEF, N_A, and N_M) was associated with variation in prior budworm density, the effects of systematic year-to-year differences, and history of recent treatment with an insecticide. Consistently, only a minor proportion of the residual variation in these dependent variables was associated with indices of site and stand conditions (section 5.2.7). From these results, I infer that both the duration and the intensity of a budworm outbreak are primarily a function of the systematic year-to-year changes in survival that are thought to result from host responses to defoliation (section 5.2.3) and from interstand redistribution (principally, of eggs) (section 5.2.2). Apparently, variation in site and stand attributes serves mainly to modify the action of these major processes.

Significantly, in their review of silvicultural tactics for reducing vulnerability to eastern budworm, Blum and MacLean (1984) concluded as follows: "...only one general association appears to be consistent—mature or overmature stands with a high proportion of balsam fir tend to be the most vulnerable." In western forests, survival of early instars was often higher in older stands (section 4.3.3.7), and the proportion of true fir in the overstory appears to be a reliable index of high budworm-related vulnerability. In NMEX, white fir consistently sustained heavier defoliation than nearby Douglas-fir (fig. 26). And in IDA, defoliation and the proportion of true fir in the stand increased together (fig. 25). In both the Northwest and the Southwest, budworm-related damage (growth loss, top kill, and overstory mortality) in multispecies stands appears to be lower on Douglas-fir than on the true firs (Bousfield and Williams 1977, Franc and others 1973, Ollieu and others 1977, Stein and McDonnell 1982, Williams 1966).

More than other budworm hosts, Engelmann spruce appears to vary in relative vulnerability to defoliation. In NMEX, the proportion of spruce foliage in the overstory was

inversely related to defoliation, and Rogers (1984) reported that Douglas-fir was more heavily damaged than either spruce or white fir in DAMAG. Further, even though spruce was positively associated with defoliation in IDA, and Williams (1966) reported more damage to spruce than to Douglas-fir in eastern Oregon, Franc and others (1973) found less growth effect on Engelmann spruce than on Douglas-fir on the Clearwater National Forest, Idaho.

Finally, Kemp and Moody (1984) found not only an inverse relation between available soil moisture and outbreak frequency, but also derived results that "...suggest that host trees growing in areas with significant volcanic ash deposits may have fewer problems with available moisture...."

Sources and sinks—In previous sections, I have described several sinks for eggs (section 5.2.2.1), suggested that massive outflights might be particularly likely in areas that had incurred heavy defoliation for the past two or three years in succession (section 5.2.2.2), suggested that inflights by migrating moths are directly related to the proportion of Douglas-fir foliage in the overstory (section 5.2.2.4), and suggested that one kind of sink may be represented by forested areas that are bounded on their upwind side by fairly wide expanses of either nonforest land or nonhost stands (section 5.2.2.4).

Outbreak duration—Once an outbreak is under way, systematic year-to-year reductions occur in three properties: the survival rate from eggs to fourth instar (section 4.3); the intensity of defoliation that ensues from any given larval density (section 4.4); and the survival rate from fourth instar to adults (section 4.5). In the absence of net gains through migration, these multiyear phenomena suggest that generation survival (S_G) may often be insufficient to maintain a stable-state density after an outbreak has persisted for five or six years. Paradoxically, the reduced survival that occurs during early instars also tends to ensure that the subsequent budworm population will not exhaust its food supply.

Weather—During an extended outbreak, defoliation may intensify as a consequence of warm, dry weather during May, June, and July (Hard and others 1980, sections 4.3.3.8, 4.6.3.9). Although high early larval survival is associated with cooler than average temperatures during March, results from my analysis of the WXBASE records suggests that outbreaks are likely to be short-lived in areas characterized by particularly cool, wet weather during May. And Fellin and Schmidt (1973), in western Montana, reported that unseasonably low temperatures in June (as low as -6 °C) probably reduced budworm survival by more than 90 percent.

In addition, Thomson and others (1984) found that the collapse of two of the five outbreaks they studied in British Columbia was associated with extremely high temperatures after moth flights.

5.3.1.3 Hazard dynamics—Commonly, data sets used to rate stand hazard from forest defoliators have used defoliation as their dependent variable, and have focused on local site and stand attributes for indices of underlying processes that reflect pest-related hazard (Hedden and others 1981, Wulf 1985). Typically, hazard-rating schemes have been used to project pest-related vulnerability to damage (Hedden 1981, Witter 1985), and have served well in this capacity (Hertel 1981). Unfortunately, our current understanding of the processes that determine budworm population dynamics suggests that results derived from these data sets cannot be extrapolated to pre-outbreak conditions, for reasons described below.

First, susceptibility to budworm outbreaks and vulnerability to subsequent damage are determined by some processes that are virtually identical and some that are very different. For example, predation processes play their principal role in determining susceptibility before significant defoliation has occurred, processes that govern interstand dispersal have a major influence on both pre-outbreak susceptibility and subsequent vulnerability, and host defenses appear to be activated primarily as responses to defoliation that is occurring or that has already occurred.

Second, interstand dispersal of adult moths is a function not only of conditions in both the stand or stands of origin and destination, but also of on-site conditions in the intervening area. Because dispersal flights of the eastern budworm occur across distances at least as great as 450 km (Dobesberger and others 1983), the areas involved in some dispersal flights of the closely related western budworm may be enormous.

Third, once an outbreak starts, the defoliation that ensues from any given budworm density during any given year is clearly a function of both the duration and the prior intensity of that outbreak. Thus, a given intensity of defoliation can imply any of a wide range of budworm densities, depending on past outbreak history.

Fourth, once an outbreak has ended, even otherwise highly susceptible stands may appear to be highly resistant for a few years, because of a residual effect from the defensive host response to the preceding outbreak.

Fifth, aerially classified defoliation provides a general index of population density in places where some defoliation is visible (Heller and Schmiege 1962). Below detection thresholds, however, such surveys provide no information for evaluating possible changes in budworm numbers. Thus, maps based on such observations can "...accentuate the illusion of...sudden changes...between endemic and epidemic levels" (Régnière 1985).

For all the above reasons, I hope that investigators will exercise restraint in interpreting underlying causes of stand susceptibility to the western budworm from observations of defoliation.

5.3.2 Assessing Defoliation Potential and Population Trend

...fluctuations in insect populations take place at different average densities in different environments, and...outbreaks may be encouraged by certain edaphic factors....Elucidation...using...density as the dependent variable and [edaphic factors] as independent variables... calls for a [sampling] design...between extensive survey and intensive population dynamics...."

—From "Annual Review of Entomology" R.F. Morris (1960)

Pest-management specialists often use aerial surveys to derive preliminary estimates of budworm activity over geographic areas covering thousands of square kilometers. Commonly, ground-based surveys are then used to supplement and support the original aerial-survey results. For the latter surveys, the area to be sampled is usually one or more geographically distinct parcels of land, such as a valley or drainage (Twardus 1985).

5.3.2.1 Ground surveys—In evaluating the potential utility of ground surveys for the western budworm, managers who contemplate using any of the equations presented here to assess either defoliation potential or population trend should consider several factors.

First, budworm density is always a key predictor variable. Second, systematic year-to-year differences in budworm survival are ubiquitous and important sources of variation in projected outcomes. As infestations age, projections of both subsequent defoliation and population trend should be adjusted downward.

Third, during prolonged outbreaks, preceding egg-mass density may provide reasonably reliable estimates of both defoliation and subsequent egg-mass density—at least for the prolonged outbreaks in this study. To achieve adequate precision in relatively new outbreaks (such as those in DAMAG or OREG), however, projections based on egg masses should be supplemented by subsequent projections based on larvae.

Fourth, the results of this study strongly suggest that budworm-forest relations may differ in important ways from region to region. During extended outbreaks, for example, mean S_s was lower in MONT than in either IDA or NMEX. Wherever possible, managers should use equations based on (or calibrated for) results derived from the same physiographic region.

Fifth, the benefits that can be derived from data on on-site attributes appear large in relation to their cost. For example, L.E. Stipe used budgetary data presented in Stipe and others (1983) and Dohrmann (1988) to estimate an average annual cost of data accumulation per three-tree cluster in MONT and a subsequent, similar study in Oregon at about $1,420 (in 1988 dollars). Using this average, it would cost about $1,661,000 to assemble the component parts of the 1,170 skeletal life tables used in this study that were derived from projects conducted by Forest Pest Management personnel in Idaho and the USDA Forest Service (IDA, MONT, NMEX, and DAMAG). Compared to this cost, the additional cost to acquire the data on both on-site attributes and interstand influences was trivial.

5.3.2.2 Lower crown beating—Recently, R. Mason and others (1989) and Mason and Beckwith (1990) described a quick and efficient method for sampling larval density in the lower crown that should suffice for estimating density before final control/no control decisions are made. The method assumes a consistent relation between larval density on low-growing foliage and average density per unit of foliage area on the whole tree. For this method, which one person can carry out, low-growing foliage is foliage that can be reached without a pole-pruner. Possibly, field trials will prove that this "lower crown beating" method can also provide acceptable whole-tree density estimates for suboutbreak eastern budworm populations. If the method does prove to be acceptable for assessing eastern budworm density, it would undoubtedly be both less expensive to apply and more environmentally acceptable than an alternative method recently proposed by Crawford and others (1990) for estimating larval densities in suboutbreak populations of this species.

5.3.3
Treatment Options

When I first went to live in San Pedro Tlaquepaque,... I was under the mistaken impression that my Mexican neighbors had nothing but dung heaps and a few trees in the yards behind their homes. As I lived there longer ..., I realized that many of these dung heaps were carefully managed gardens and orchards. ...There was no problem of erosion ... humidity would be kept up during the dry season and plants of the same sort were so isolated from one another by inter-vening vegetation that pests and diseases could not readily spread....
—From "Plants, Man and Life"
by Edgar Anderson (1952)

5.3.3.1 Direct suppression—According to Stipe (1987), about 5 000 000 ha in the Western United States were treated with DDT for budworm suppression between 1949 and 1964. Since that time, managers have tested a variety of chemical and bacterial insecticides and behavioral chemicals (Fellin 1983, Stipe 1987). Except for the recent operational program in Washington and Oregon, however, the large-scale treatments of the 1950s and early 1960s have not been repeated. Simply put, large-scale treatment of the western budworm has been discontinued in much of the interior West primarily because the results of the early treatments were disappointing (Fellin 1983, Fellin and Shea 1985). Although short-term objectives to reduce populations were commonly met, subsequent population resurgence obliterated these apparent gains.

Now, several findings suggest that managers should reevaluate treatment policies for the western budworm, at least in some situations. First, S_s was much lower in areas where budworm outbreaks were prolonged (IDA, MONT, and NMEX) than in nonoutbreak areas, and S_s systematically declined across the course of outbreaks in both OREG and DAMAG. Second, annual declines in S_L across the outbreak in OREG were very similar to those noted earlier in S_s. Third, in three areas subjected to prolonged outbreaks, survival during posttreatment years was lower in treated blocks than in nearby check blocks. Fourth, as already noted, other investigators (Dimond and Morris 1984) have suggested that pesticides may be more effective against the eastern budworm after an outbreak has persisted for several years. Together, these findings suggest that the hosts of the western budworm react to defoliation by a heightened production of defen-sive chemicals. If the hosts of the western budworm react to repeated defoliation by a heightened defense, then these trees might be even more resistant if they could be relieved of defoliation pressures for one or two growing seasons. As Buffam (1985) noted, once an outbreak starts "...spraying remains the only viable alternative for reduc-ing losses...." Other authors echo this same conclusion for both the eastern and western budworms (Carter 1987, Flexner and others 1983). In prolonged outbreaks, treatment with an appropriate insecticide might be deliberately timed to complement and magnify host defenses.

Unfortunately, the apparent east-to-west decline in host defensive ability during out-breaks (section 5.2.3.4) suggests not only that defoliation per prior egg will be much higher in westerly outbreaks, but also that host responses to prior insecticide treatment will be lower. Recently, reports of substantial host mortality in the Blue Mountains of eastern Oregon, together with studies on the results of insecticide treatment in this same area (Gillespie 1990; Torgersen and others, manuscript in review; Wickman and Torgersen 1991), appear to confirm these gloomy suggestions. Consequently, manag-ers who contemplate using an insecticide against a budworm outbreak in Oregon or

Idaho should plan to treat early in the outbreak. Particularly in this westerly area, managers may also want to consider the kind of preemptive treatment that McLeod (1979) described for the numerically bimodal life system of the Swaine jack pine sawfly, *Neodiprion swainei* Middleton.

5.3.3.2 Silvicultural treatment—The western budworm outbreaks I studied exhibited minor, inconsistent, and unstable relations between forest attributes and budworm survival (section 5.2.7). Clearly, these results undermine recent assumptions that current knowledge is sufficient to formulate and recommend silvicultural treatments as a generally applicable management solution in budworm-susceptible forests. Nevertheless, silvicultural treatments can unquestionably reduce susceptibility to budworm in individual stands. Carlson and Wulf (1989) describe silvicultural tactics to "...reduce the proportion of host, capitalize on resistant genotypes, regulate stand density so that growth is optimized and vigor is improved, improve conditions for budworm predators, and reduce rotation length." To support or amend these tactics, the material presented here has confirmed or revealed that: (a) budworm moths tend to favor Douglas-fir for oviposition (section 4.6.3.8); (b) during an outbreak in a mixed conifer stand, true firs will suffer the most defoliation (section 4.4.3.7); (c) within a generation, budworm survival tends to increase with both increasing stand age and increasing variation in crown depth (sections 4.3.3.7, 4.5.3.4, and 4.6.3.8); and (d) except on sites where moisture is limiting, budworm survival is inversely related to shrub density (section 4.6.3.8). Also, findings just discussed (section 5.3.3.1) suggest that the effectiveness of host reactions to defoliation are directly related to the vigor of the stands under attack. These findings, in turn, suggest that silvicultural measures designed to increase stand vigor during interludes between outbreaks should pay off during subsequent outbreaks by a heightened ability of the trees to respond to attack. Carlson and others (1985b) noted that the defensive chemistry of fir in á thinned budworm-infested Douglas-fir/ponderosa pine stand may have been enhanced by thinning.

Various constraints in many western forests "...dictate the use of uneven-aged management" (Schmidt 1985), and current trends suggest these constraints may soon extend to most of the publicly owned forest land in the Western United States. Even without these constraints, Fellin and Dewey (1982) caution that "managing budworm infestations by silviculture...is not practical in many western forests." Rather than simply tolerating persistent budworm outbreaks on such forests, some managers may wish to consider treatment with an appropriate insecticide timed to enhance host defenses (section 5.3.3.1). Also, fire ranks next to climate in shaping the age, composition, and structure of interior western forests (Wellner 1978b). Managers who hope to restore fire to its natural role should consider the benefits that would accrue to other areas from using fire to reduce the hazard these forests may represent as sources for budworm outbreaks. In this regard, consider that McCullough and Kulman (1991) found that survival of the jack pine budworm in northwest Wisconsin was "...likely to be lower on trees regenerating after wildfire than on trees regenerating after clearcutting. Low budworm survival was consistently associated with reduced foliar nitrogen on trees in the burned areas.

5.3.3.3 Enhancing predation—Significantly, timber yields are not among the goods and services projected from a large portion of our publicly owned, budworm-susceptible western forests (Carlson and Wulf 1989). On such forests, tactics designed to reduce the budworm problem through most silvicultural activities or to save on-site timber by suppressing outbreaks with insecticides are inappropriate. Paradoxically, because management options on such forests are so limited, these forests provide a magnificent opportunity to test assertions such as the one advanced by Hassell (1978) that "...pests

of...forest trees are particularly amenable to biological control...." Specifically, these forests appear to offer an excellent opportunity to evaluate and use the management potential inherent in predaceous birds and foliage-foraging ants.

According to Clausen (1940), "Ants were the first group of insects utilized in an attempt to control insect pests by the biological method. For centuries, the date growers of Yemen have brought ant colonies from the hills and placed them in the trees for protection...." In European forests, ants in the *Formica rufa* group are routinely moved from site to site. In Canada, investigators have successfully moved colonies of both European and North American foliage-foraging ant species both intra- and intercontinentally (Bradley 1972; Finnegan 1975, 1977). On forests where wood production is not a management objective, such as many interior forests, certain possible drawbacks that might otherwise arise from enhancing ants are not relevant. (For example, aphid populations may increase in the presence of ants [Skinner and Whittaker 1981]; ants may cause degradation in tree boles [Sanders 1970, Simeone and others 1988]; and ant-induced lesions may be suitable infection courts for pathogenic fungi [Houston 1969]). Similarly, although maximizing habitat patchiness may be virtually impossible in such forests, following some of Langelier and Garton's (1986) other suggestions for increasing populations of birds seems advisable, such as creating snags, or providing nesting boxes, water, and salt. Significantly, even in a northern Washington forest without specific management practices to encourage avian predators, Takekawa and Garton (1984) estimated that the effect of avian predators on the western budworm was worth at least $1,820 per km² per year over a 100-year rotation. As Youngs (1983) concluded,

> Perhaps a complex of ant species would provide more effective control...than a single dominant species, and different complexes may be more successful in controlling pests that are widely distributed....Perhaps, also, silvicultural manipulations—such as those that open the stand or create more woody debris for nesting sites—can augment ant populations without costly colony transplantation. But all these possibilities remain mere speculation until more research is done.

5.3.4 Human Activities and the Budworm Life Systems

Attempts to eliminate uncertainty are delusory and often counterproductive. The appropriate concept for both assessment and policy design is a recognition of the inevitability of uncertainties and the consequent selective risk-taking.
—From "Adaptive Environmental Assessment and Management"
C.S. Holling, editor (1978)

In this century, eastern budworm outbreaks have occurred more frequently than in the past. Outbreaks also have coalesced and increased in area (Blais 1985). And in the West, Swetnam and Lynch (1989) noted a similar pattern. In both cases, the investigators postulated that the increased budworm activity was due to human activities. In eastern forests, Blais (1985) cites pulpwood harvesting, fire prevention, and insecticide use as primary causes. In the West, many authors (Carlson and Wulf 1989, Carlson and others 1985a, Schmidt 1987, Swetnam and Lynch 1989) cite timber harvesting and fire suppression.

In a review of eastern budworm population dynamics, Mattson and others (1988) suggested that the recent numerical behavior of eastern budworm may represent a

relatively sustained period of movement around the outbreak equilibrium position of the dual equilibrium model described in Morris (1963c). They suggested further that these high-density oscillations could go on indefinitely as long as a sufficient number of susceptible stands are not allowed to die from severe defoliation. These authors concluded that "...successful interaction of the spruce budworm with its hosts seems to depend on the quality and organization of the host plant landscape."

The material discussed in section 5.2.2 refutes the notion advanced by Carlson and others (1985a) that "...adult budworm in the northern Rocky Mountains are believed to move only a short distance from the stands in which they pupated." In fact, redistribution of eggs by gravid moths is a dominant process in maintaining forest-wide western budworm outbreaks.

Clearly, budworm-related management actions in any given stand or entomological unit can have major effects on budworm dynamics across a much larger area. I believe that future planners for forest-wide budworm-related management should make such interstand relations a linchpin in developing their strategies. To borrow a recommendation from the literature on managing agroecosystems (Price and Waldbauer 1975),

> ...planning of the spatial relationships of crops and uncultivated land should be done at the ecosystem level, in anticipation of insect movements over a period of years in relation to their densities in crops, prevailing winds, and cultural practices.

As noted by Blum and MacLean (1984), a regional management strategy for budworm-susceptible forests should include "...protection and silvicultural treatments of particular geographic areas that may act as focal points for initiation of outbreaks, reservoir areas, or mass dispersal routes for budworm moths."

To develop an effective forest-wide management strategy against the western budworm, managers should consider a tactical mix of a range of activities that includes doing nothing, direct suppression of budworm outbreaks, silvicultural treatments, and predator enhancement. Further, to fully implement integrated pest management (IPM), this tactical mix should be supported by a package that assists managers to evaluate potential interactions among specific tactics, weather, other pests, and other forest values. For example, carbaryl spraying intended to reduce western budworm populations has also been shown to reduce both ant species diversity and foraging, at least temporarily. As Murphy and Croft (1990) concluded "...reduced ant predation after spraying could contribute to [budworm] resurgence...." Unlike carbaryl, most victims of B.t. are lepidopterous larvae (Dimond and Morris 1984). Thus, the use of B.t. should not have drastic unintended effects on this important predator guild.

Significantly, IPM continues to be the policy of the USDA Forest Service for dealing with forest pests (USDA 1990). Components of a first-generation attempt to develop an IPM decision-support capability for managers who must deal with forests susceptible to the western budworm are noted in Stark and Wright (1987).

Fortunately, patterns of timber harvesting, fire management, and insecticide use are largely subject to the deliberate control that can be imposed by forest land managers. Increasingly, land-use policies in budworm-susceptible forests incorporate projections of the possible budworm-related consequences of contemplated actions (Simmons and others 1984, Stage and others 1985). Obviously, these projections are imperfect.

Nevertheless, some uncertainty of outcome is universal for managers, who are thus "...used to choosing between various options ... to resolve some issue in a limited time frame" (Cuff and Walker 1985). By incorporating budworm-related considerations in a larger planning context, managers can minimize both the crisis-management environment that has characterized "budworm management" in the past (Knight 1981) and the danger that inputs from a single area of concern will dominate resource decision-making (Baskerville 1977). In short, managers who apply appropriate forest management practices may well be able to minimize budworm problems on many western forests, a sustaining goal of at least a segment of the forest entomology community for many years (Graham and Knight 1965, McFadden and Campbell 1978, Stark 1971). As Knauer (1991) put it,

> ... we have only two options: work together and...[provide] promised IPM strategies; or go on with the status quo and wait for the public and policy makers to become disenchanted....

Unlike deliberate management activities, some other human actions that may alter the budworm life systems are far beyond the direct reach of an on-site manager. Among these actions, Holling (1988) included a reduction in avian predators as a consequence of tropical deforestation, industrial pollution, and actions that increase climatic variability. As we attempt to consider the effects of these and other global forces on system behavior, the principal threat posed by such forces seems likely to be through their potential to transform whole ecosystems. As Holling (1988) pointed out,

> ...the budworm/forest system is remarkably resilient...stability domains are large and the variables within them can fluctuate extensively...[and] regulatory processes...are remarkably robust to external change. Ironically...great resilience and robustness... mask slow erosion of...capacity to renew and...leave managers ill-prepared for surprises.

Above all, managers and planners need to be able to identify activity patterns that are likely to reduce the resilience of ecosystems.

5.4 Usefulness of Historical Records

When the population dynamics of a single species is known for different competitive situations under different ecological conditions throughout its geographic range, ecologists will begin to have some insight into the relationship of that species to its environment.
—From "Ecological Monographs"
J.A. Organ (1961)

In 1982, when I began to assemble the records that are the basis for this paper, I was intrigued by the prospect that they might yield hundreds or even thousands of skeletal but (I hoped) useful life tables. Obviously, the information gleaned from these records and presented here has led to more questions than answers about underlying processes. In fact, if knowledge of processes is the goal, then I must agree with the scientists cited by Régnière (1985): "...scientists actively studying spruce budworm population dynamics believe that it will be more useful to seek an explanation of historical records from basic knowledge of the underlying mechanisms, rather than the other way around."

I, on the other hand, believe that a formal periodic investigation of the historical record is justified for reasons discussed in the following sections.

**5.4.1
Saving and
Enhancing Records**

Retrospective investigations can assimilate and synthesize the results of prior studies. As Jeffers (1982) wrote: "Especially where much of the research is undertaken by different groups of people, and in different locations...integration... becomes an important task." Further, users of historical data may find uses that were not contemplated by those who did the original work. By assembling records from an array of sources, an analyst can sometimes derive an overview of the system that was not available to the original investigators. For example, even fragmentary records may reveal slow-acting processes or processes with substantial time lags, if those records represent a sufficient interval. Such processes, acting over decades, can be crucial in ecosystem changes (Magnuson 1990).

Periodic retrospective studies would also reduce record losses. To be analyzable, historical records have to be available. Time after time, in searching for a particular group of potentially useful records, my search ended with the discovery that those records had been lost or discarded.

In fact, most of the records used here were acquired in projects to evaluate the efficacy of an insecticide. Traditionally, designers of such projects do not include elucidating pest population dynamics among their objectives. For concurrent or retrospective studies on population dynamics, the results of my study suggest that the value of such records would be hugely enhanced by a modest further set of mutually acceptable interregional sampling protocols.

**5.4.2
Research, Development,
and Application**

In summarizing information about the population dynamics of the eastern budworm, Blais (1985) noted that conclusions derived from one region and during one outbreak "...do not necessarily apply at large. It is dangerous to generalize on studies limited in time and place." Certainly, the results reported here both support Blais' advice for that insect and extend it to the western budworm. To understand similarities and differences between regions and outbreaks, Blais suggests forming several multidisciplinary groups "...to gain knowledge of the basic principles associated with...[budworm] ecology...."

Fortunately, although process-oriented studies can ramify endlessly, synthesis of the historical records can provide logical priorities for a competing array of such studies. Specifically, although historical records may not suffice to identify underlying processes, they do provide an excellent basis for generating hypotheses about such processes. As McNamee and others (1981) pointed out "simple, easily gathered biological information is sufficient to describe the equilibrium structure and temporal behavior of a system." Empirically derived results from several projects can reveal major phenomena that had previously been overlooked and suggest their probable causal pathways. They can also limit the plausible role or roles of many candidate processes and eliminate other processes from further consideration.

For obvious reasons, funds adequate to conduct either a major pilot control project (such as MONT or NMEX) or a research and development program (such as the CANUSA Spruce Budworms Program) are only likely to be committed to studies on a handful of our most destructive forest pests. For these few pests, Campbell and McFadden (1977) noted that ongoing research and development programs provide an opportunity to assimilate and synthesize the results of prior studies.

With or without a full-scale research and development program, the results of this study suggest that records documenting pilot control projects can sometimes be coupled with

records documenting population research to provide key elements of an empirical basis for either reinforcing or altering currently held theories about a pest's population dynamics. Even if this information is only useful for planning, the evaluators of several prior research and development programs on forest pests (Cleland and others 1979) recommended that "Future planning for an accelerated program should include...a thorough review of...existing background technology...[and should 'package' this information in readily usable form] before the program begins." In fact, the results of my retrospective study both refute a substantial number of widely held notions about the population dynamics of the western budworm and raise many new questions. Clearly, these results have supplied many of the components needed to construct a new research and development campaign against this pest. Similarly, although the eastern budworm is surely one of the world's most studied organisms (Knight 1981), information on the population dynamics of the insect "...is far from complete, and some of it is controversial" (Blais 1985). Perhaps retrospective studies for the eastern and the jack pine budworms similar to the one described here for the western budworm would fill in some of the gaps in current understanding of these life systems, or at least limit the plausible roles of some candidate processes. Certainly, the mass of historical records on the eastern budworm life system must dwarf the records I was able to assemble for this retrospective study on the population dynamics of the western budworm. At the least, a synthesis of these records would provide more comprehensive descriptions of numerical patterns in each of those budworms and thus a rational framework for comparably comprehensive theories of their dynamics.

Meanwhile, knowledge of processes is **not** the only goal of applied research. Information useful to managers and planners can often be derived even when the nature of underlying processes remains uncertain. Currently, for example, the results of this study have yielded information that both supplements existing guidelines and furnishes some new ones to managers who deal with budworm-susceptible forests. In the future, I assume that much of this new information will be incorporated in regionally calibrated and management-oriented models.

5.5 Study Limitations

Even the best field studies...suffer from ecological deficiencies and statistical inadequacies which inevitably result in conclusions being matters of personal opinion and not of incontrovertible fact.
—From "Cold Spring Harbor Symposium on Quantitative Biology" A. Milne (1957)

Thanks primarily to sustained efforts by Forest Pest Management, an abundance of useful data has been accumulated on populations of the western budworm. Inevitably, however, certain attributes of the collective data base constrain the potential applicability of derived results. Some of these constraints are summarized below:

Eggs per mass—In most of the projects, estimates of EG are based on relations between EG and N_M that were found in MONT (section 4.3.1). Contrary to experience with other insects, EG increased in MONT within each of two successive years across an extremely broad range in N_M. Without further data, I can only speculate on the generality or uniqueness of this relation.

Emerging moths—Estimates of N_A in several projects are based on relations found in COLO, PNW, and SAMP (section 4.6.1). This relation does not reflect the systematic decline in S_L across a multiyear outbreak that was found in OREG. If further studies show that systematic changes in S_L are universal during extended outbreaks, such changes can be incorporated in an equation to derive more realistic values for N_A in projects such as IDA, MONT, NMEX, and DAMAG.

Environmental indices—The descriptions of forest conditions used in this study were acquired through a series of very rough estimates. In the future, more useful equations could be derived by combining budworm and defoliation data with more precise estimates of the environmental attributes that have been shown to be statistically significant. In addition, indices need to be developed that better reflect mortality-causing processes in sparse populations, interstand movements by gravid moths, and the intensity of host defenses induced by defoliation.

Weather—Better data are needed to refine relations between weather and budworm survival in natural populations. Ideally, these data will accrue through a long-term study designed to satisfy this need.

Sparse populations—To my knowledge, no sustained attempt has been made to describe the numerical behavior of a western budworm population during an extended innocuous phase. In contrast, exhaustive (and, undoubtedly, exhausting!) foliage sampling has shown that eastern budworm populations sometimes reach extraordinarily low densities between outbreaks (perhaps as low as 0.01 larva per m^2 of foliage (section 4.7.3.2). By using grids of pheromone-baited traps (Allen and others 1986, Grant 1991, Sartwell and others 1985) and arrays of selective whole-tree exclosures, such as those in Campbell and others (1983b), future investigators may be able to resolve some of these low-density concerns, without having to collect and examine thousands of square meters of foliage.

Silvicultural measures—More than 95 percent of the data used in this study were drawn from budworm outbreaks. Obviously, Forest Pest Management has a responsibility to pay attention to outbreaks. Nevertheless, it seems ironic that more than 95 percent of the population data on this pest have been collected from situations that probably represent less than 5 percent of all the budworm populations in host forests.

Recent years have seen a major thrust to deal with budworm-susceptible forests through silvicultural measures (Carlson and Wulf 1989, McFadden 1979, Schmidt 1985). Unfortunately, much of the technical support basis for silvicultural recommendations in such forests has been derived by extrapolating from results acquired during outbreaks. Because such extrapolation can be misleading (section 5.3.1.1), increased knowledge of budworm-habitat relations during nonoutbreaks is needed. As Blum and MacLean (1984) pointed out for the eastern budworm, "...pontificating about...silvicultural 'control'...is based on a combination of faith...logic...scientific evidence and...experience," and to progress in developing effective silvicultural strategies we need "...quantitative relationships that can be tested in the real world...."

In summarizing the effects of silvicultural practices on forest pests, G. Mason and others (1989) noted that "The most effective approach for reducing pest-caused damage...is to focus on low pest populations...." Ideally, the growing union between silviculture and forest pest management will allow pest management specialists to devote as much time to studying nonoutbreak populations as they have spent on outbreaks.

6
Recommendations

*If the only alternative to an overly simple model is an elaborate frame-
work of guesses, nothing much has been gained.*
**—From "Mathematical Ecology"
by E.C. Pielou (1977)**

IPM implies a compatible blending of three elements: management practices, the natural processes of pest control, and uncertainty. Unfortunately, in attempting to develop IPM, the element of uncertainty has often been managed badly. What starts out as a plausible hypothesis may soon be perceived as established truth, a mistake that can block the very paths that would lead to better management. In short, an investigator must be willing to say "I don't know."

6.1
Historical Records

A major body of untapped information is undoubtedly contained in the records that continue to accumulate about our forest pests. Currently, investigators who propose to use such records in retrospective studies may be frustrated by the following problems: (1) identifying studies that contain relevant information; (2) finding stored and ignored records; (3) coping with the lack of a subset of variables common to several data sets, preventing full use of otherwise valuable records; and (4) specifying realistic objectives, which may be impossible until after the available records have been identified, acquired, assembled, and evaluated. A few suggestions follow.

- Many studies that contain potentially valuable information are not identified in the published record. To alleviate this problem, I think that an annotated catalog should be assembled for each of our major North American forest pests that identifies and describes the records that document all population studies, pilot control projects, damage assessments, and related work.

- The loss of most of the gypsy moth-related Melrose Highlands records during a disastrous fire at the Forest Insect and Disease Laboratory in New Haven, Connecticut, is a reminder (Campbell 1967) that records can be lost even when they are known to be worth saving. Both to minimize such losses in the future and to make the information broadly available, I think that forest management organizations should publish more of their data and not just summarize results. Model publications include the sequence of annual reports on the New Mexico Control Project, which begins with Parker and others (1978), and the report by Stein and McDonnell (1982) on the New Mexico Damage Assessment Project.

- A lot of money is spent to obtain reliable estimates of pest population density. Frequently, however, a sampling technique developed in one area may be modified to accommodate conditions, objectives, or constraints in another area (Allen and others 1984). To ensure that these estimates will be fully usable, I think that North American forest research and management organizations should agree on a common minimal subset of variables for each major pest and include estimates of these common variables in all subsequent population studies and projects.

- Several time-consuming steps may have to be completed before realistic objectives can even be specified for a retrospective study. First, the study may have to begin with a search for relevant records. Second, once identified, the records have to be acquired and assembled. Third, the assembled data have to be evaluated to get a preliminary idea about their strengths and their shortcomings. Sadly, research managers do not smile on projects that require such a long gestation before the investigators can even

specify what they hope to achieve. To alleviate this problem, I think that major retrospective studies could be authorized in a sequence of two or more parts. For example, authorization to identify, acquire, and assemble relevant historical records should provide a basis for subsequent decisions about the assembled data.

6.2 Budworm Population Dynamics

In a critique of several research and development programs on major forest pests, Allen and others (1982) noted that "...fiscal constraints and public demands for accountability indicate that researchers can no longer either pursue `hobbies' or devote many years to every detail of a pest's ecology." Also, as Gilbert (1976) pointed out, ascertaining that an outbreak may occur is not enough. Projections are also required on both likely outbreak-related effects and the efficacy of possible controls.

Despite all of these problems, managers must have several packages of budworm-related population information to fully implement the pest management philosophy of the USDA Forest Service in budworm-susceptible stands. First, to make intelligent budworm-related decisions, managers need a working knowledge of the processes that dominate year-to-year changes in budworm numbers. Second, to derive optimal results from management activities, managers need to be able to project the likely consequences of these activities on the numerical behavior of subsequent budworm generations. Third, managers need a device that will allow them to put budworm-related activities in a larger planning context.

The results in this paper suggest several studies that will be required to fully implement pest management in budworm-susceptible forests. These recommended studies support and extend Mitchell's (1987) recommendations for further work on the population ecology of the western budworm. In addition, the decision-support system projected earlier for this pest (McFadden 1979, Twardus and Brookes 1983, Wickman 1976) has now incorporated many untested hypotheses about various aspects of budworm population dynamics, including several hypotheses that are not supported by the results of this study— for example, elements in Carlson and others (1985a), Sheehan and others (1989), Stark and Wright (1987), and Wulf and Cates (1987). The recommended studies provide a basis for testing and modifying many of these elements, and for developing and testing components for an improved IPM system.

In addition, the results of this study strongly suggest that the principal differences among the dynamics of the genetically similar populations of the western, eastern, and jack pine budworms arise from differences among their host sites, stands, and communities of natural enemies, together with systematic differences in weather among the three pest distributions. Thus, the interspecies patterns and comparisons displayed in figures 43, 46, 48, 51, and 54 suggest many opportunities to optimize the value of individual study results through a deliberate series of comparable studies on the population dynamics of all three pests. In particular, continent-wide trends in components of the budworm life systems, across a wide range in densities, could provide an effective way to monitor northern and alpine terrestrial environments for possible changes in ecosystem resilience. Realistically, some of these studies will require a coordinated interregional effort. Here are some suggested objectives for such an effort and a procedural framework for reaching them.

6.2.1 Population Processes and Environmental Influences

The dynamics of the budworm populations reported here exhibited several major attributes that refute commonly accepted notions. To ensure that appropriate budworm-related management decisions will be made in budworm-susceptible forests, further

information is needed on certain population attributes and processes known to be important and on more precise ways to project the consequences of these attributes.

Objective 1: Evaluate the roles of predation, macro-parasitism, and disease in the dynamics of sparse populations.

Background—Some process or processes commonly maintain populations of both the eastern and western budworms at sparse densities. In the Northwest, exclosure trials show that predation by birds and ants provides a low stable equilibrium density. In eastern forests, stomach analyses of feeding birds also suggest that birds play a major role in sparse populations, but exclosure trials have yielded equivocal results. In the Southwest, only fragmentary studies have been conducted on these processes.

Recommendation—Conduct standardized exclosure trials and acquire standardized estimates of density and mortality-by-cause on about 12 sites in each of five regions (Pacific Northwest, northern Rockies, southern Rockies, Lake States, and Maine). In Canada, equivalent regions might be British Columbia, the Prairie Provinces, Ontario, Quebec, and the Maritime Provinces.

Objective 2: Assemble a basis for projecting within-generation survival in sparse populations as a function of both resident budworm density and characteristics of sites and stands.

Background—In both eastern and western forests, susceptibility to budworm outbreaks and vulnerability to subsequent damage are determined by some processes that are identical and some that are very different. Thus, attempts to deduce causes of susceptibility from observations of outbreak phenomena (such as defoliation) can be misleading. Unfortunately, such attempts currently provide most of the basis for recommended silvicultural treatments of budworm-susceptible forests.

Recommendation—Acquire standardized estimates of both density and site and stand characteristics on about 30 sites in each of the five specified regions. **Note**: In each region, 12 of these sites could also be used to achieve objective 1.

Objective 3: Evaluate the roles of interstand migration by gravid moths in the release of sparse populations to outbreaks, the year-to-year maintenance of outbreaks, and declines from outbreaks to sparse populations.

Background—In both eastern and western forests, immigration of gravid moths commonly exceeds the combined effects of emigration and on-site moth mortality. In western forests, several documented outbreaks would almost certainly have declined without occasional massive migration. In both eastern and western forests, however, the role of moth migration in budworm dynamics continues to be in dispute.

Recommendation—Acquire standardized estimates of density, including moth catches in pheromone-baited traps, from about 25 sample points in each of 12 sites (6 sparse and 6 outbreak) in each of the five specified regions. **Note**: In each region, the six sparse sites used here could also be among those used to achieve objectives 1 and 2.

Objective 4: Assemble a basis for projecting sources and sinks for gravid moths as a function of both site and stand characteristics and interstand attributes.

Background—Site and stand attributes have a major influence on where female moths deposit their eggs. In the West, at least, some areas appear to be chronic "sinks" for gravid moths. Conversely, some evidence suggests that even a chronic sink may occasionally be the source of a massive outflight.

Recommendation—Acquire standardized data on defoliation, site and stand characteristics, and interstand influences from each of the specific sampling points, sites, and regions used to reach objective 3.

Objective 5: Evaluate the role of host responses induced by defoliation in budworm population dynamics.

Background—In the West, the survival rate of small larvae changes from a relatively high and constant rate at the start of an outbreak to a relatively low, density-dependent one as the outbreak progresses. This pattern is consistent with findings that some host foliage becomes toxic to the pest as an outbreak progresses. Declining values of both defoliation and large larval survival also occur during outbreaks and appear to be functions of declining foliage quality. Apparently, defoliation activates some sort of defensive responses by the host trees. Some of these patterns also appear to occur in the life systems of both the jack pine with jack pine budworm and the balsam fir with eastern budworm.

Recommendation—Acquire and freeze foliage samples from each site used to reach objectives (3) and (4). Depending on population trends, bioassay these samples for insights into underlying processes.

**6.2.2
Evaluating Treatment
Efficacy**

To select appropriate management tactics and develop optimal total strategies, managers need a quantitative basis from which to project the budworm-related consequences of various possible management actions. Much of this quantitative basis still remains to be developed.

Objective 6: Evaluate the efficacy of various silvicultural options in maintaining budworm populations at sparse densities.

Background—Unlike the standardized protocols used to evaluate insecticides, no equivalent protocols exist for evaluating the efficacy of silvicultural treatments in modifying budworm dynamics. Further, in both eastern and western forests, the vast majority of current silvicultural guidelines for keeping populations sparse have been extrapolated from studies based on outbreaks.

Recommendation—Acquire standardized estimates of both density and within-generation survival in sparse populations on at least three replicates of each silvicultural treatment widely used in budworm-susceptible forests in each of the five specified regions. **Note**: In each region, data accumulated to reach objective 2 could provide baseline survival rates for untreated stands.

Objective 7: Evaluate the role of host responses to defoliation in determining insecticide efficacy during posttreatment years.

Background—In Montana, New Mexico, and Idaho, western budworm survival during posttreatment years was consistently lower in blocks that had been treated with an

insecticide. This difference in budworm survival between treated and untreated blocks is thought to arise from defensive responses to defoliation by the host trees. Similar but weaker posttreatment responses after insecticide treatment have also been noted in the life system of the eastern budworm. To my knowledge, insecticide applications have never been deliberately timed to complement such host responses.

Recommendation—Conduct standardized insecticide trials in a new outbreak (3 treatment blocks and 12 check blocks) in each of the specified regions. Assuming that the outbreak persists, treat three of the check blocks each year for each of three subsequent years. Maintain density and defoliation records on all blocks for six years. In addition, accumulate and freeze foliage samples from each block. Depending on results, bioassay these samples for insights into underlying processes.

6.2.3 Modeling Budworm Dynamics

Decision-support systems that provide managers with the ability to test a variety of management alternatives in a model of the ecosystem have become "the heart" of IPM (Berryman 1986). Because of their central position, the models imbedded in these decision-support systems must yield reasonably accurate projections.

Objective 8: Validate and improve current models for DEF, EG, N_L, N_A, and N_M, and calibrate them for each of the specified regions.

Background—In this work, I have described projection capabilities for both defoliation and four successive western budworm densities (eggs per mass, fourth instars, emerging moths, and egg masses). Within limits set by the data, each projection capability summarizes relations found between one of the above dependent variables and influences in the following categories: attributes of sites and stands, density dependence, interstand influences, weather, systematic year-to-year differences, and influences of insecticide treatment.

Recommendation—Ensure that objectives 1 through 7 are met. Together, they provide the information needed to reach this objective.

Objective 9: Develop and field-test a regionally calibrated and management-oriented model of budworm population dynamics.

Background—At present, western managers can either use a model that "...simulates the processes that affect budworm population dynamics in great detail" (Sheehan and others 1987), or they can virtually ignore budworm dynamics, assume a particular outbreak duration, and use their best guess about expected defoliation.

Recommendation—As Holling (1978) noted, "A simple but well-understood model is the best interface between a complex system and a complex range of policies." The analyses in this paper were intended to provide much of the basis for just such a model. First, this model should be developed. Second, it should be field-tested and calibrated against the information assembled to reach objectives 1 through 8.

7

Summary

7.1
The Study

A study of the population dynamics of the western budworm was begun in 1982. The data, gathered from historical records, were collected between 1959 and 1988 during nine unrelated projects scattered across interior forests in six western States (Washington, Oregon, Idaho, Montana, Colorado, and New Mexico). These data were analyzed to produce projection capabilities for both defoliation and four successive budworm densities [eggs per mass (EG), fourth instars (N_L) emerging moths (N_A), and egg masses (N_M)]. Within limits set by the data, each projection capability summarizes relations found between one of the above variables and influences in the following categories: attributes of sites and stands, density dependence, interstand influences, weather, systematic year-to-year differences, and influences of insecticide treatment. The study also compares several age-interval survival rates among the principal North American needle-eating budworms (Chapters 2, 3, section 4.7).

7.2
Comparisons Among
Budworm Species

Across an outbreak, generation survival in populations of eastern, western, and jack pine budworms shows similar systematic year-to-year declines, even though the life system of the eastern budworm may not include the property that systematically depresses S_S (= N_L/N_E) in the western budworm and, possibly, the jack pine budworm as well. Results based on data that include trends in new outbreaks show that S_L (= N_A/N_L) in eastern budworm populations continued to increase at densities well beyond where it was rapidly declining in the western budworm. Across lower densities, S_L in the eastern budworm appears similar to that found in both the western and the jack pine budworms. Apparently, the life system of the eastern budworm contains little evolutionary advantage for the short-lived balsam fir to invest in chemical defenses. In possible contrast, the evidence suggests that changes in host-defense chemistry are the most likely causes for the systematic year-to-year reductions in both S_S and S_L across the course of western budworm outbreaks (section 5.2.3).

In all three species, interstand redistribution of eggs by fecund moths is a common event. Contrary to Royama's (1984) hypothesis that eastern budworm populations have only one equilibrium point, the evidence suggests that populations of both the eastern and western budworms have two major population modes, outbreak and sparse, and two transient phases, release and decline (sections 4.7 and 5.2.8.5).

7.3
The Western Budworm

The data—The data base provided 1,251 western budworm life tables. Each life table included an estimate of egg masses at the start of generation n ($N_{M(n)}$), eggs per mass (EG), fourth instars (N_L), emerging moths (N_A), and egg masses at the start of generation n + 1 ($N_{M(n+1)}$). In individual plots, nonzero egg density per m² ranged from 2.2 to 12,667; S_S (= N_L/N_E) ranged from 0.0003 to 4.85; S_L (= N_A/N_L) ranged from 0.007 to 0.76; and S_A (= N_M/N_A) ranged from 0.01 to 1,811. In all projects, large variances were found in both starting density and subsequent survival rates, as compared to the variance in density at the end of the generation. Covariances shared between pairs of independent variables usually made important contributions to variance at the end of the generation (section 4.1).

Overview—In larger data sets, a subset of three to five independent variables was consistently associated with almost as much of the variation in any given dependent variable as the full set of statistically significant predictors. Almost invariably, prior density and indices of systematic differences from year to year were the first two variables to enter the equations. An index of prior treatment was the only other variable to enter more than a few models. Clearly, western budworm population dynamics are dominated by density-dependent processes, by those that vary systematically from year to year, and occasionally by weather (section 5.2).

Density and natural enemies—Even when western budworm outbreaks are wide-spread, some process or processes maintain the populations on at least 95 percent of the total western host forest at densities where they are scarcely noticed. In the Northwest, results of exclosure trials show that the combined effects of predaceous birds and ants provide a lower stable equilibrium budworm density, which should persist until other processes raise survival above replacement densities (sections 4.5.3.1, 5.2.1.2).

Density and moth behavior—Site and stand attributes have a major influence on where female western budworm moths deposit their eggs. Commonly, immigration of gravid moths greatly exceeded the combined effects of emigration and on-site moth mortality. The low generation survival in both MONT and NMEX suggests that both outbreaks would have declined without occasional massive immigration. Apparently, these areas serve as "sinks" for gravid moths. The results suggest that a mass moth exodus took place from DAMAG in both 1982 and 1983 and from MONT in 1983. In both of these areas, the presumed mass outflight was preceded by at least two years during which defoliation was severe and S_A clearly exceeded the egg-laying potential of on-site emerging moths. Results from several projects (IDA, MONT, NMEX, and DAMAG) suggest that major flights by gravid western budworm moths may travel much farther than has generally been supposed, possibly 450 km or more (sections 4.6.3.3, 4.6.3.6, 5.2.2).

Density and induced defenses—In prolonged outbreaks, small western budworm larvae are subjected to severe density-dependent mortality. In nonoutbreaks, S_S was virtually constant. Apparently, S_S transitions from a relatively high constant rate at the start of an outbreak to a relatively low density-dependent one as the outbreak progresses. In prolonged outbreaks, the pattern of early-instar mortality is consistent with Perry and Pitman's (1983) finding that some host foliage is toxic to the budworm. Declining values of both defoliation and S_L also occur during prolonged outbreaks, and they also appear to be functions of declining foliage quality. Large year-to-year differences in the relation between an index of outbreak intensity and survival provide further support for the hypothesis that defoliation activates some sort of defensive response by the host trees (sections 4.3.3.1, 4.3.3.3, 4.3.3.5, 4.4.3.1, 4.4.3.3, 4.4.3.5, 4.5.3.2, 4.6.3.1, 4.6.3.3, 4.6.3.6, and 5.2.3).

Density and the herbivore community—During western budworm outbreaks, densities of its foliage-eating associates usually remain sparse. In other ecosystems (northern hardwoods, for example), simultaneous outbreaks by several defoliators are common, and loss of effective control by the defoliator's natural enemies would be catastrophic. (section 5.2.4).

Host responses to insecticide treatment—Three projects (IDA, MONT, and NMEX) included a sequence of observations on both treated and untreated blocks. Consistently, western budworm performance (as measured by S_S, DEF, and S_A) was lower in the treated blocks during posttreatment years. I was unable to find empirical evidence to disprove the hypothesis that the difference in budworm performance between treated and untreated blocks is a function of differential host-tree response to the two situations (sections 4.3.3.4, 4.4.3.4, 4.6.3.4, and 5.2.5).

Weather—Western budworm survival in Montana was reduced when mean January temperature was extremely low (below about -13 °C), but it also varied inversely with temperature in March. Survival was also depressed at all mean May temperatures below about 8.8 °C, and it dropped dramatically when mean May temperature was below about

5.7 °C. Survival was also lower when mean June temperatures were not appreciably warmer than those in May. Survival was depressed by rainy days in May, but it was also lower when total precipitation for May and June was very low (less than about 8.4 cm), and it was higher when precipitation during May, June, and July was between 10.5 and 14 cm. Thus, the relation between spring and summer droughtiness and budworm survival in Montana could be represented by a dome-shaped curve (sections 4.3.3.8, 4.6.3.9, and 5.2.6).

Environmental modifiers—Generally, only minor correlations were found between the western budworm and various environmental indices. Complicating factors in this regard include various autocorrelations among the indices, mass interstand flights by gravid females, and failure to formulate meaningful indices (section 5.2.7).

Population modes and phases.

• Most western budworm outbreaks may be triggered by migrants, presumably from ongoing outbreaks (sections 4.6, 5.2.8.1).

• Prolonged, low-intensity outbreaks appear to be maintained when strongly density-dependent mortality develops among the early instars. In such outbreaks, low values of S_s ensure that few larvae will reach fourth instar, regardless of possible moth inflights and consequent high initial egg density (sections 4.3.3.1, 4.3.3.3, 4.4.3.3, and 5.2.8.2).

• Before a prolonged outbreak develops, most outbreaks may collapse through systematic year-to-year declines in both S_s and S_L. The evidence strongly suggests that some of these declines are precipitated primarily by changes in host foliage, as induced by prior defoliation. Even under chronic outbreak conditions, adverse weather—particularly a series of cool, wet intervals in May—would probably cause an outbreak to collapse (sections 4.3.3.1, 4.3.3.8, 4.5.3.2, and 5.2.8.3).

• Predaceous birds and ants can stabilize most western budworm populations at innocuous densities, at least in the Northwest (section 5.2.8.4).

Limitations—Several attributes of the collective western budworm data base constrain the applicability of the derived results. In particular, at least 95 percent of these data were drawn from outbreaks. Unfortunately, extrapolation to nonoutbreaks from results acquired during outbreaks can be misleading. We need, therefore, to increase our knowledge of budworm-habitat relations during nonoutbreaks (sections 5.3.1 and 5.5).

**7.4
Study Implications**

Population science.

• Investigators should consider numerical patterns of population change as they evaluate the possible role of any given process in a population they are studying. For example, host responses to herbivory can be expected to result in cyclic herbivore behavior only in life systems where other limiting processes are generally ineffective (section 5.2.10).

• Each of the three conifer-eating budworm species discussed here is limited by processes that operate through three different trophic levels, i.e., producer, herbivore, and carnivore.

- The foliage-eating insects that periodically escape control by natural enemies often appear to be distinguished by density-related behavioral traits that allow them to overcome these low-density controls.

- The results of this study show that samples drawn from midcrown tips together with information on intrastand patterns of western budworm occurrence (Campbell and others 1984a) can provide an acceptable sequence of density estimates for many studies on the population dynamics of this pest (section 5.2.9).

Management.

- Susceptibility to budworm outbreaks and vulnerability to damage are determined by some processes that are identical and some that are very different. Thus, attempts to deduce underlying causes of stand susceptibility from observations of outbreak phenomena (such as defoliation) can be misleading. Factors that influence susceptibility, those that influence vulnerability, and those that influence both are described in section 5.3.1.

- Factors are described that should be considered by managers who contemplate using equations presented in this paper to assess either defoliation potential or population trend in western budworm (sections 4.3.3.2, 4.4.3.2, 4.6.3.2, and 5.3.2).

- In considering direct suppression, planners should deliberately time insecticide treatment to complement and magnify host defenses.

- The results of this study tend to confirm or modify existing recommendations for silvicultural treatments to reduce budworm-related problems, at least for individual stands.

- Publicly owned western forests deemed to be susceptible to budworm and in which timber yields are not contemplated offer an excellent opportunity to evaluate and use the management potential inherent in generalist natural enemies.

- Most important, planners need to develop forest-wide strategies that use a variety of tactical means to cope with the hazards posed by interstand movements of eggs by gravid moths (section 5.3).

Using historical records—Together, records documenting pilot control projects on the western budworm and those documenting population research provide a basis for reinforcing some current theories and altering others about the population dynamics of the western, eastern, and jack pine budworms. Because this information is useful to managers, planners, and research scientists, I believe that formal periodic investigations of other such records would also be justified (section 5.4).

7.5 Recommendations

Necessarily, several packages of population information lie at the core of integrated pest management. Inevitably, flaws in this information may limit or even mislead efforts to manage any given pest. For example, untested hypotheses in the current decision-support material for the western budworm could lead to management decisions that subsequently prove to have some unfortunate consequences. For the life systems of all three budworms, an efficient way to both test such hypotheses and improve core information packages may be through a retrospective study that uses existing population records, followed by a coordinated interregional research and development effort. Through such an effort, it may be possible to identify activity patterns that are likely to reduce resilience in the ecosystems that include these herbivorous pests, or at least to detect such reductions before they become irreversible (Chapter 6).

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To Sandy Campbell,
1936-1992
in loving memory

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